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Development of the Cephalic Lateral Line Nerves of the Japanese Anchovy, *Engraulis japonicus*

Seiji Ohshimo

Bull. Seikai Natl. Fish. Res. Inst., (77), 1-10 (1999)

Development of the cephalic laterel line nerves of the Japanese anchovy was observed using the two histological staining methods, sudan black B and hematoxyline-eosin. In the early larval stage (about 10 mm SL: Standard Length), the infraorbital nerve was only stained by sudan black B, and the facial ganglia were observed. The infraorbital, supraorbital, mandibular, preopercular, supratemporal, and posterior lateral line nerves were seen at the stage of over 20 mm SL. The nervous system of the Japanese anchovy is concluded to be established over 20 mm SL, with especially the fine nerves being well developed in the rostral region.

Key words: anchovy, *Engraulis japonicus*, brain nerves, lateral line

Influence of Fish Diurnal Behavior on Acoustic Biomass Estimation

Seiji Ohshimo, Osamu Katoh and Kenji Morinaga

Bull. Seikai Natl. Fish. Res. Inst., (77), 11-22 (1999)

The influence of diurnal fish behaviors on its biomass estimations was studied using acoustic methods, an ADCP and a quantitative echo sounder. The survey was carried out during 11th to 15th January 1994 with the R/V Yoko-maru, and four transects were executed off the western coast of Kyushu. The acoustical data of ADCP and quantitative echo sounder were collected by a new method using four round-trip surveys along each on a transect with a length of about 30 miles during a time period of 24 hours and 50 minutes. Additionally, CTD casts were conducted at an interval of about 3 nautical miles on each transect. A coastal front was formed in the eastern part of the transect between the Goto Islands and Kyushu, and a southward current was clearly observed there. Many fish schools were clearly observed at the coastal front in the Goto-Nada. The estimated biomass varied in a day. In the present study, the acoustic problems resulting from fish behavior were discussed quantitatively.

Key words: acoustic survey, fish behavior, biomass estimation,

Developmental and Comparative Morphology of Beryciform Larvae (Teleostei : Acanthomorpha), with Comments on Trachichthyoid Relationships

Yoshinobu Konishi

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The morphological development of nine beryciform larvae, *Beryx* sp., *Anoplogaster cornuta, Diretmoides pauciradiatus, Diretmichthys parini, Anomalops katoptron, Monocentris japonicus, Aulotrachichthys* sp., *Hoplostethus* sp. and *Gephyroberyx japonicus*, and larval polymixiiform, *Polymixia* sp., is described and illustrated. The striking characters shared by these larvae are well developed head ornamentation with bony ridges and spines. Other features, such as body shape, anus position, prolonged fin rays, abdominal scutes, hyoid barbels, incipient luminous organs, and pigmentation on the body and pelvic fin are useful for identification of the postflexion larvae of the ten species. Cladistic analysis of relationships among the Anoplogastridae, Diretmidae, Anomalopidae, Monocentridae and Trachichthyidae using larval and some adult characters corroborates hypotheses based only on adult characters that these five families are a monophyletic assemblage, anoplogastrids and diretmids are sister groups, and the Trachichthyoidei are monophyletic. The analysis also suggests that anomalopids and monocentrids are sister taxa, and the Trachichthyidae are paraphyletic.

Key words : Teleostei, Beryciformes, larvae, development, relationships

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Seiji Ohshimo*

ABSTRACT

Development of the cephalic laterel line nerves of the Japanese anchovy was observed using the two histological staining methods, sudan black B and hematoxyline-eosin. In the early larval stage (about 10 mm SL: Standard Length), the infraorbital nerve was only stained by sudan black B, and the trigeminal ganglia were observed. The infraorbital, supraorbital, mandibular, preopercular, supratemporal, and posterior lateral line nerves were seen at the stage of over 20 mm SL. The nervous system of the Japanese anchovy is concluded to be established over 20 mm SL, with especially the fine nerves being well developed in the rostral region.

INTRODUCTION

Generally in the teleost fishes, the morphology of the central nervous system is related to the behavioral pattern (Uchihashi, 1953; Brandstätter and Kotrschal, 1990) and the peripheral nervous system in the cyprinid fishes has been shown to be differ between habitats (Illick, 1956). The morphogenesis of the central nervous system of the red seabream, *Pagrus major*, and Japanese eel, *Anguilla japonica*, change ontogenetically, and these changes are considerd to enhance the survival of the larvae (Toyoda and Uematsu, 1994; Tomoda and Uematsu, 1996). Ogawa (1967) reported on the morphogenesis of the brain of the Japanese anchovy *Engraulis japonicus*, and related morphological changes to the behavioral development. However, he did not report on the morphogenesis of the peripheral nervous system of the Japanese anchovy. Pfeilar (1989) reported that the morphological changes of the peripheral nerves during the metamorphosis, so it is important to describe the morphological changes of nervous system for understanding the fish

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behavior.

In the clupeoids, the sensory canals and cranial lateral line nerve have been studied in the Atlantic herring, *Clupea harengus* (Blaxter *et al.*, 1983), Gulf menhaden, *Brevoortia patronus* (Gunter and Demoran, 1961), gizzard shad, *Dorosoma cepedianum* (Stephens, 1985), and in the family Engraulidae (Nelson, 1983; Nelson, 1984). Furthermore, there are studies on the development of the peripheral innervations of the cephalic region in the Atlantic menhaden, *Brevoortia tyrannus* (Hoss and Blaxter, 1982), and the Atlantic herring (Blaxter *et al.*, 1983). All clupeoid fishes metamorphose during the life time, subsequently, behavioral patterns may change during metamorphosis. In the present study, the development pattern of the lateral line nerves of the Japanese anchovy was observed using histological methods to clarify the development of behavior, especially feeding behavior.

MATERIALS AND METHODS

Adults (>60 mm Standard Length; SL), juveniles (≧35 mm) and larvae (<35 mm) of the Japanese anchovy were collected by midwater trawling or plankton net (NORPAC net) in the waters off the western coast of Kyushu, Japan. The sampled specimens were fixed immediately in 10% formaldehyde or in a neutral bufferd 10% formaldehyde solution (pH 7.4). All of the fish were re–fixed in a neutral buffered 10% formaldehyde solution within 24 hours after sorting. A sub–sample was preserved in 70% ethanol. All fish measurements referred to in this paper are as standard lengths (SL), i.e., from the tip of the snout to the end of the hypural.

For the histological studies, fishes were immersed in Bouin's solution for one week. After dehydration, the specimens were embedded in paraffin, cut to make 10 μm sections using a microtome, and stained with hematoxyline–eosin (HE). Sections were observed under a light microscope.

For the sudan black B method, the eyes and gut were carefully removed with the optic nerve intact. All specimens were then immersed in a water bath for between 1 hour to several days in order to remove the formaldehyde or alcohol. The specimens were macerated with trypsin (Difco) for between 2 hours to 1 week at 37℃. The macerated and cleared specimens were then dipped in saturated sudan black B (Merck) in 70% ethanol for 2 hours. After staining, the specimens were transferred to 70% ethanol for several seconds, and then immediately immersed in 40% ethanol. The specimens were carefully squeezed in 40% ethanol, and bleached until the nerves became clear in the same solution. Finally, the specimens were observed under a dissecting microscope using a *camera lucida* and

sketches drawn. A part of the fishes, the skeletons and nerves were stained by alizarine red S, alcian blue and sudan black B, respectively.

RESULTS

1) Adult and juvenile stage

In the adult stage, the supraorbital (=ophthalamic branch) and infraorbital (=maxillary branch) nerves coursed above and below the eye, respectively (Fig. 1 and Fig. 2). Both nerves were well developed in the rostral region, and the supraorbital and infraorbital nerves innervated to the nasal capsule. The infraorbital nerve branched below the eye, and the branched nerve rostro–caudal extended in the upper jaw. Furthermore, the infraorbital nerve branched in the ventro–caudal region, and the branched nerve (horizontal nerve) joined to the

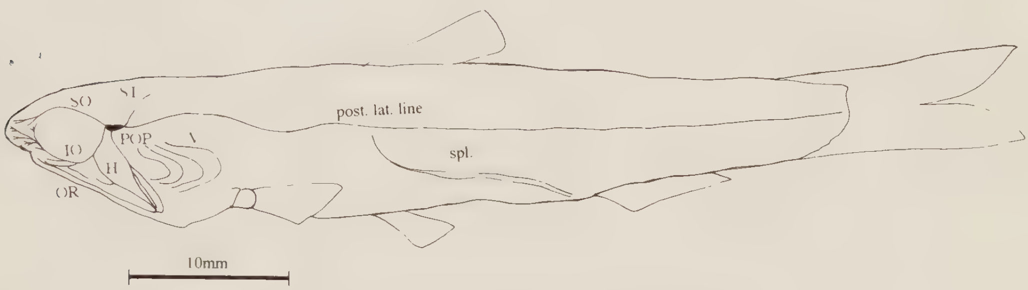


Fig. 1. The cephalic and trunk lateral line nerves of a juvenile (52.0 mm SL) anchovy. H: horizontal nerve; IO: infraorbital (=maxillary) nerve; OR: oral (=mandibular) nerve; POP: preopercular nerve; post. lat. line: posterior lateral line nerve; SO: supraorbital (=ophthalamic) nerve; spl.: splanchnic nerve; ST: supratemporal nerve; V: vagal nerve.

preopercular nerve. The preopercular nerve run through the cheek region and reached to the articulatio mandibularis. The oral nerve (=mandibular branch) rostrally coursed along the lower jaw (Fig. 1 and Fig. 2). The supraorbital, infraorbital and preopercular nerves arose from the trigeminal ganglion. The posterior lateral line and supratemporal nerves arised from the facial ganglion. The posterior lateral line nerve reached to the caudal end of the body. Figure 2 shows the skeleton of the neurocranium and splanchnocranium, and typical nervous pattern in the cephalic region.

2) Larval stage

In about 10 mm SL larva, the infraorbital and vagal nerves were observed using sudan black B stain (Fig. 3A). The trigeminal ganglion and the infraorbital

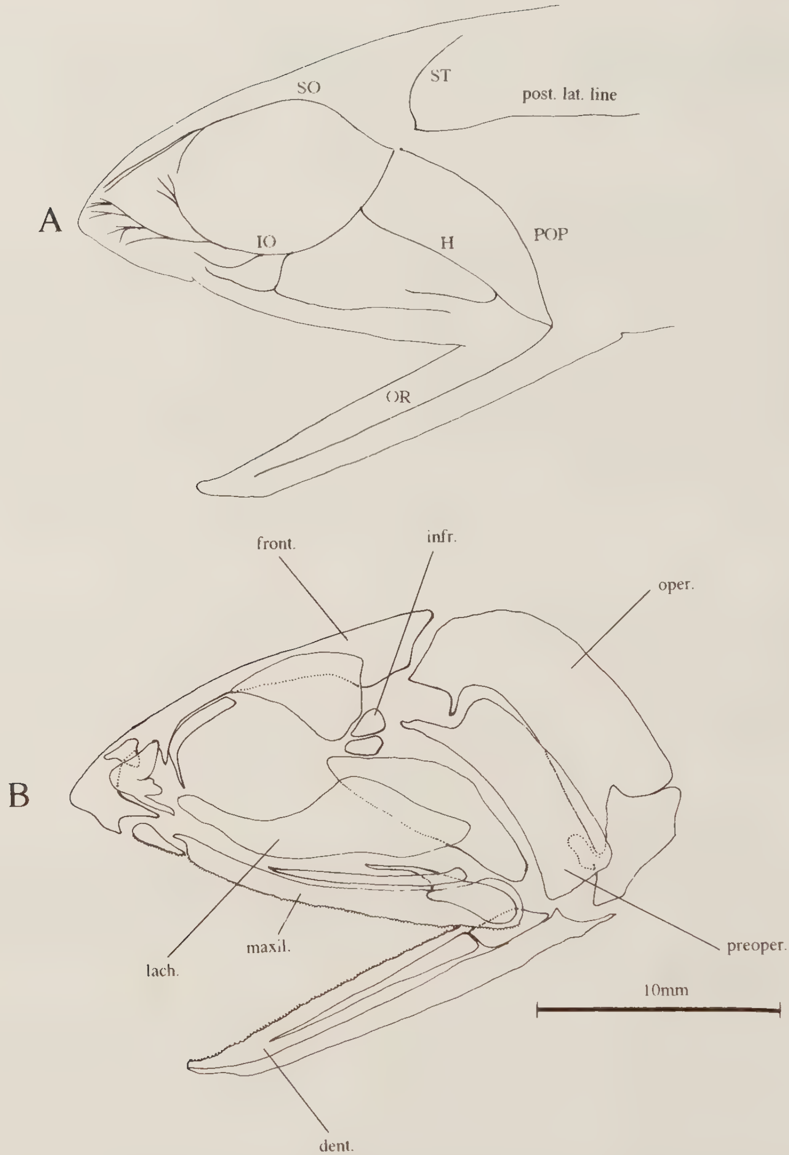


Fig. 2. The typical cepalic lateral line nerves (A), and the skeleton of the neurocranium and splancnocranium (B) of an adult (91.5 mm SL) anchovy.
dent.: dental bone; H: horizontal nerve; IO: infraorbital (=maxillary) nerve; infra.: infraorbital bone; front. frontal bone; lach.: lachrymal bone; maxil. : maxillary bone; oper.: opercular bone; preoper.: preopercular bone; OR: oral (=mandibular) nerve; POP: preopercular nerve; post. lat. line: posterior lateral line nerve; SO: supraorbital (=ophthalamic) nerve; ST: supratemporal nerve.

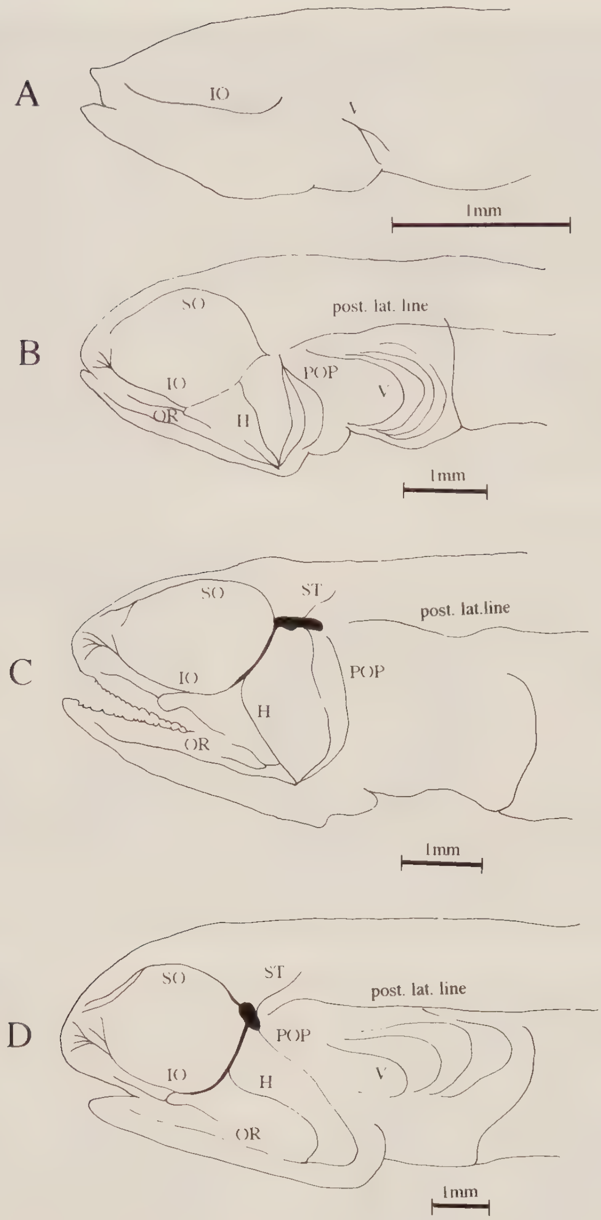


Fig. 3. Development patten of the cephalic lateral line nerves in the larval stage.
(A) 12.0 mm SL, (B) 21.8 mm SL, (C) 25.5 mm SL, (D) 34.7 mm SL
H: horizontal nerve; IO: infraorbital (=maxillary) nerve; OR: oral (=mandibular) nerve; POP: preopercular nerve; post. lat. line: posterior lateral line nerve; SO: supraorbital (=ophthalamic) nerve; ST: supratemporal nerve; V: vagal nerve.

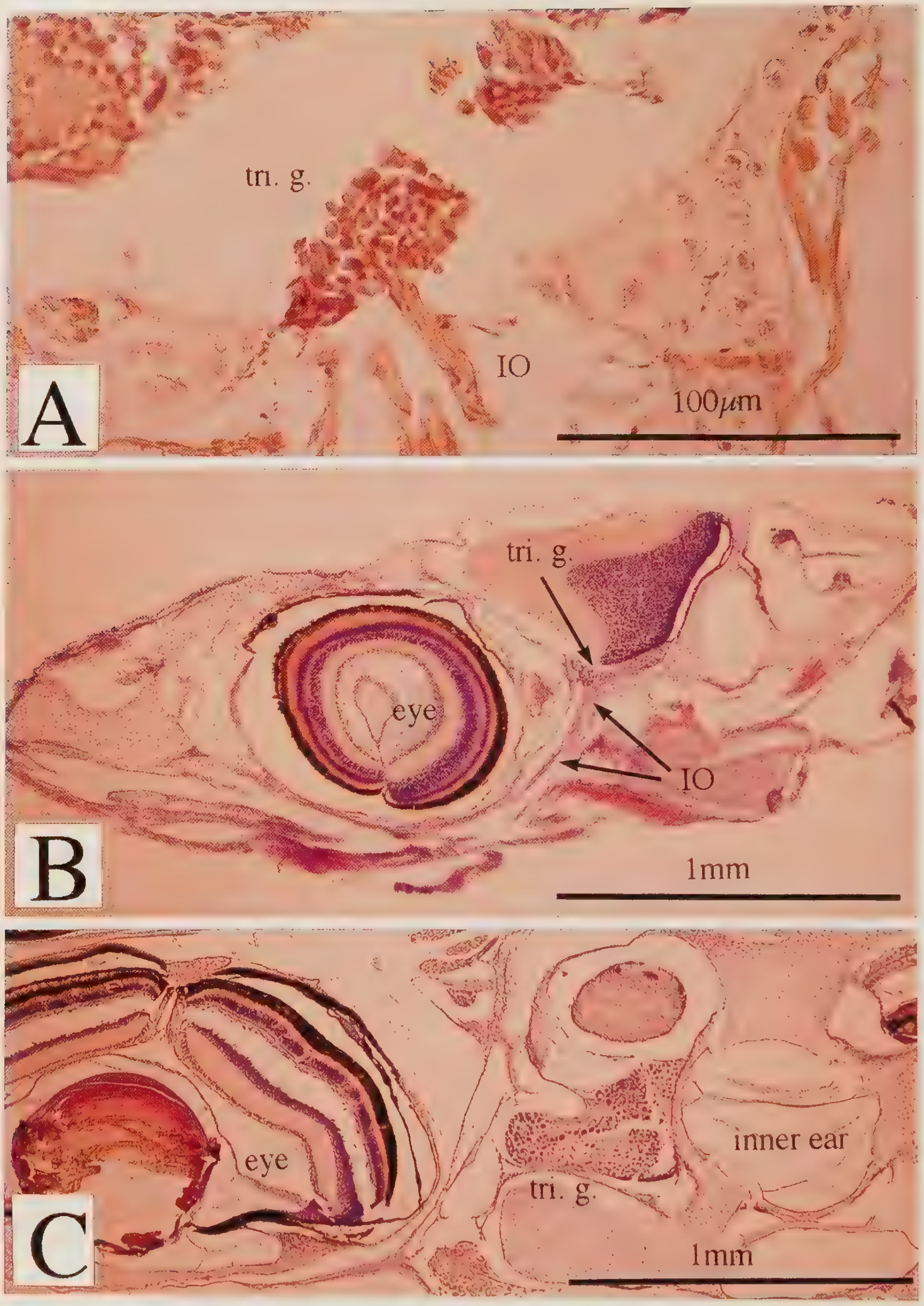


Fig. 4. The cephalic nerves and trigeminal ganglion in larval anchovy.
A: The trigeminal ganglion (tri. g.) and infraorbital nerve (IO) was observed in a 9.6 mm SL. B: The infraorbital nerve arised from the trigeminal ganglion and course below the eye in a 17.1 mm SL specimen. C: The cell number and size of the trigeminal ganglion developed in a 33.5 mm SL specimen.

nerve were also seen in a 9.6 mm SL larva (Fig. 4A), however, the ganlion's cells were small and few, and the infraorbital nerve was fine. The trigeminal ganglion and the infraorbital nerve were clearly observed in a 17.1 mm larva (Fig. 4B). In a larva over 20 mm, the supraorbital, infraorbital, preopercular, oral, supratemporal and posterior lateral line nerves were already developed readily observable using sudan black B stain and HE stain (Fig. 3B, and Fig. 4C). The vagal nerves, innervated to the gills, were also clearly seen. In a 25.5 mm larva, the cephalic nerves were already established (Fig. 3C, D).

DISCUSSION

Clupeomorphs are one of the most abundant fish groups on earth, and are known from fossils to date as far back as the early Cretaceous (Grande, 1985). The cephalic sensory canals of the Clupeidae is remarkably free from the bones, and spreads through the opercular and subopercular region (Gunter and Demoran, 1961). In addition, most species of Engraulidae are characterized by an unusually prominent pig-like snout projecting beyond the tip of the lower jaw with the mesethmoid projecting in front of the vomer and supporting a paired sensory rostral organ (Nelson, 1994). The cranial lateral line nerve of the Engraulidae has been described by Nelson (1984). However, there is no report on development of the cephalic lateral line nervous system in the Japanese anchovy. In the present study, the development of the cephalic nerves of the Japanese anchovy are described in order to clarify behavioral development with growth.

The mechanosensory organs in the initial stages of teleostean fishes are almost free of neuromasts, and the ontogenetic development of the free neuromasts and lateral line has been reviewed by Blaxter (1987). The primary neuromasts develop from placodes on the head region. They give rise to both canal neuromasts and free neuromasts (Blaxter and Fuiman, 1989). In the Clupeiformes, there are reports of the free neuromasts in the larval stages, i.e., northern anchovy, *Engraulis mordax* (O'Connell, 1981), Japanese anchovy (Iwai, 1983), Atlantic herring (Blaxter *et al.*, 1983), and Atlantic menhaden (Hoss and Blaxter, 1982). In addition, the organization of the neuromasts into lateral line canal systems occurs later in development: for example, at a body length of 18 to 20 mm in northern anchovy (O'Connell, 1981), 17 mm in Atlantic menhaden (Hoss and Blaxter, 1982), and 24 to 26 mm in Atlantic herring (Blaxter *et al.*, 1983). In the present study, the infraorbital nerve was only observed at the length of about 10 mm SL, and the nervous pattern of the Japanese anchovy was basically established by 20 mm SL. Fukuhara (1992) reported the morphogenesis of the body form, fins, and intestine

of the Japanese anchovy. The tip of the snout is pointed during the larval stage but becomes rounded when the fish reaches a length of about 20 mm SL (Fukuhara, 1992). In the present study, well developed nerves at the rostral region were observed at about 20 mm SL. The infraorbital (=maxillary) nerve, supraorbital (=ophthalamic) nerve and oral (=mandibular) nerve were consisted of the trigeminal nerve (Butler and Hodos, 1996), and the trigeminal nerve plays a role in the gustatory and mechanosensory responses. So, there is a relationship between the changes of the morphology of the tip of the snout and the development of the nerves in the rostral region, and this relationship may be related to the behavioral development in the Japanese anchovy. Then in the present study, the relationships between development of the nerves and feeding behavior are discussed.

Feeding behavior of the Japanese anchovy has examined from with gut contents (Uotani *et al.*, 1978; Uotani, 1985b), and development of the gill structure (Uotani, 1985a). In addition, the biting behavior of larva has been observed (Fukuhara, 1983; Uotani, 1985a), and feeding behavior changed to filtering behavior in adult anchovy (Fukuhara, 1983). Hunter (1972) also described the feeding behavior of larval northern anchovy, with anchovy larva catching the zooplankton in front of the snout. Uotani (1985a) reported that Japanese anchovy larvae fed on zooplankton only in the daytime. Unfortunately, there are no reports on any feeding behavior of juvenile and adult Japanese anchovy in dark conditions. As the Atlantic herring switches from biting and filtering in the light to only filtering in the dark (Batty *et al.*, 1986), it follows that Japanese anchovy could similarly capture zooplankton in the dark. If so, Japanese anchovy may obtain the ability to feed in the dark during the metamorphosis (>20 mm SL) and this feeding behavior will be related to the completion of the cephalic lateral line nerves.

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カタクチイワシの頭部側線神経の発達

大 下 誠 二

要 旨

カタクチイワシの脳神経のうち特に側線神経の発達を，スダンブラックＢ法と組織切片の検鏡を行うことで観察した．標準体長約10㎜の個体では，infraorbital（眼下）神経のみがスダンブラックＢ法で観察された．組織切片でも，infraorbital 神経と三叉神経節が観察されたが，三叉神経節は小さく、細胞数は少なかった．標準体長20㎜以上の個体になると，成魚の神経系の形態とほぼ同様となり，infraorbital 神経，supraorbital（眼上）神経，mandibular（下顎）神経，preopercular（前鰓蓋）神経，supuratemporal（側頭上）神経，posterior lateral line（後部側線）神経が観察された．特に，infraorbital 神経と supraorbital 神経は吻部で細かい神経に分岐していた．

魚類の日周行動が音響学的な現存量の評価に与える影響

大下　誠二*・加藤　修**・森永　健司*

Influence of Fish Diurnal Behavior on Acoustic Biomass Estimation

Seiji Ohshimo, Osamu Katoh and Kenji Morinaga

ABSTRACT

The influence of diurnal fish behavior on its biomass estimation was studied using acoustic methods, an ADCP (Acoustic Doppler Current Profiler) and a quantitative echo sounder. The survey was carried out during 11 to 15 January 1994 with the R/V Yoko-maru, and four transects were executed off the western coast of Kyushu. The acoustical data of ADCP and quantitative echo sounder were collected by a new method using four round-trip surveys along each on a transect with a length of about 30 miles during an time period of 24 hours and 50 minutes. Additionally, CTD casts were conducted at an interval of about 3 nautical miles on each transect. A coastal front was formed in the eastern part of a transect between the Goto Islands and Kyushu, and a southward current was clearly seen there. Many fish schools were clearly observed at the coastal front in the Goto-Nada. The estimated biomass was varied in a day. In the present study, the acoustic problems resulting from fish behavior were discussed quantitatively.

は　じ　め　に

日本の国連海洋法条約の批准および発効に伴い，日本でも1997年１月より TAC（許容漁獲量）による漁業管理制度が導入された．国連海洋法条約では，科学的に最善の手法を用いて海洋生物資源の資源量評価を行い，資源を適切に管理することが義務づけられている．資源量評価手法の一つである計量魚群探知機を用いた音響調査は，1960年代から各国で行われはじめ，計量魚群探知機の性能が高まるとともに資源量評価に欠かせない手法の一つとして定着している（例えば，Lima and Castello, 1995）ほか，中層域の生態系の解明にも役立っている（Koslow et al., 1997）．九州西岸を含む東シナ海域においても，カタクチイワシやマイ

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ワシなどの中層性小型浮魚類を対象に音響学的手法により現存量評価が行われている（Takeshita et al., 1988；Ohshimo, 1996；Ohshimo et al., 1998）．音響学的手法による現存量評価を精度よく行うためには，限られた調査日程の中でより広い海域を調査する必要があるため，昼夜を問わず調査されてきた．ところが，中層性の魚類では顕著な昼夜の鉛直移動を行うもの（Blaxter and Hunter, 1982）や，昼夜の水平移動を行うものの存在が報告されており（Robinson et al., 1995），特に表層にまで鉛直移動した場合，計量魚群探知機の測定領域からはずれるために計測することが不可能となり，現存量が過小評価されることが報告されている（Aglen, 1994）．また，底付近に分布する生物量も評価できない．このような日周鉛直移動の他にも，昼間に集群することにより，群の下方を遊泳している魚群が測定できない（シャドウ効果）ことから現存量が過小評価される（Appenzeller and Leggett, 1992）という報告もある．このように魚類の日周行動が音響学的な現存量の評価に与える影響は無視できないにもかかわらず，それを定量的に算定した報告は非常に少ない．

著者らは1994年1月九州西岸域に4本の観測定線を設定し，各定線上で海洋観測を行うとともに同一定線上での現存量の日周変化を把握するため，計量魚群探知機による一昼夜内の4往復反復調査を実施した．本報告では，九州西岸域の水塊構造と魚群分布との関係について考察するとともに，中層性魚類の日周行動が音響学的な現存量評価に及ぼす影響を定量的に評価した．

方　　法

1）海洋観測

九州西岸域に設定した観測線（A～D；Fig. 1）において，CTD（Niel Brown MK3B）による水温・塩分観測および ADCP（Acoustic Doppler Current Profiler；古野電気社製，CI－30）による流況観測を陽光丸（西海区水産研究所所属499トン）により1994年1月11～15日に実施した．ADCP の音波送受波器は陽光丸の船底に装備されており周波数は130kHz である．ADCP の結果を流速は0.1ノット単位，流向は0.1度毎に出力した．観測層は3層であり，最も浅い層は10m深に固定し，残りの2層は海深の約70%以内の範囲で適宜調整した．ADCP 観測では，観測値から潮流を除去するため，24時間50分の間に約30マイルの定線上を4往復してデータを収集する4往復調査法（加藤，1988）を適用した．各定線上には10点の CTD 観測点を設け，4往復調査法の前に水温と塩分を観測した．定線上を4往復することにより，同一地点において8個の流向・流速値が得られる．これを平均化したものを日周平均流と呼ぶ．なお，定線E・Fでは天候不良のため片道一回のみの ADCP 観測を実施した．

2）魚群分布調査

定線A，B，C，Dでは，ADCP による4往復調査と同時に，計量魚群探知機（古野電気社製 FQ－70）を用い，体積後方散乱強度（S_V 値：dB）を0.5マイル毎に収集した．なお，計量魚群探知機は調査の前に，水中ハイドロホンを用いて，電気的に較正を実施してある．得られた体積後方散乱強度は，距離約3マイルの区間毎に体積後方散乱係数 sv 値に変換した後に平均した．S_V 値と sv 値の関係は，次の式で示すことができる．

$$sv = 10^{(S_V/10)}$$

$$S_V = 10\log_{10}(sv)$$

平均化した sv 値は表層（10～20m），中層（60～80m）と全体層（10～140m）に分け，片道の航程における sv 値の積算値をその調査時間帯の値として日周的な変動を求めた．なお，本調査で使用した計量魚群探知機の周波数は50kHz であり，ADCP の使用周波数との干渉はなかった．

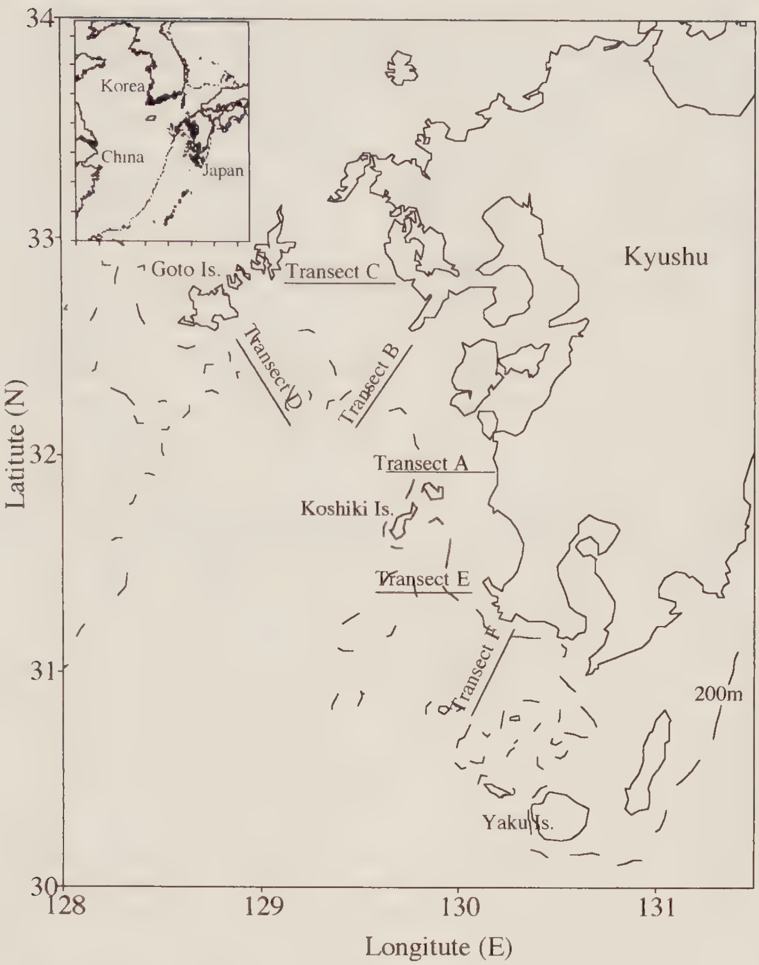


Fig. 1. Acoustic transects in the waters off west Kyushu.

結　　果

1）水塊構造と流れの分布

定線 A（天草沖海域），B（野母崎沖海域），D（五島福江島南海域）では（Fig. 2），10m深に1ノット以上の強い日周平均流が観測され，それらは200m等深線に沿うように定線 A では北向きに，定線 B，D となるにしたがって西向きになった．しかしながら，定線 C（五島灘）では1ノット以上の日周平均流は観測されず，約0.3ノットの北向きあるいは南向きの流れであった．また，定線 B の東端付近では弱いながら南向きの流れが観察された．一回のみの流向・流速の観測であるが，定線 E では定線の西（沖合）側に強い北西方向の流れが，東（沿岸）側では南向きと北向きの両方が存在すること，定線 F では概ね東向きの流れが卓越していた．

本調査期間では，観測された日周平均流がトカラ海域から甑島の沖合もしくは甑海峡を抜けて，五島福江島の南を西方向へ反時計回りに向かっていることが特徴である．しかし，この流れは，九州と五島とで挟まれた100m以浅の海域（五島灘：定線 C）には流入しないことが分かった．



Fig. 2. Diurnally averaged flow vectors at 10 m depth on transects A, B, C and D west of Kyushu in January 1994.
For transects E and F round-trip surveys were not carried out, and flow vectors are shown based on one-time current measurement.

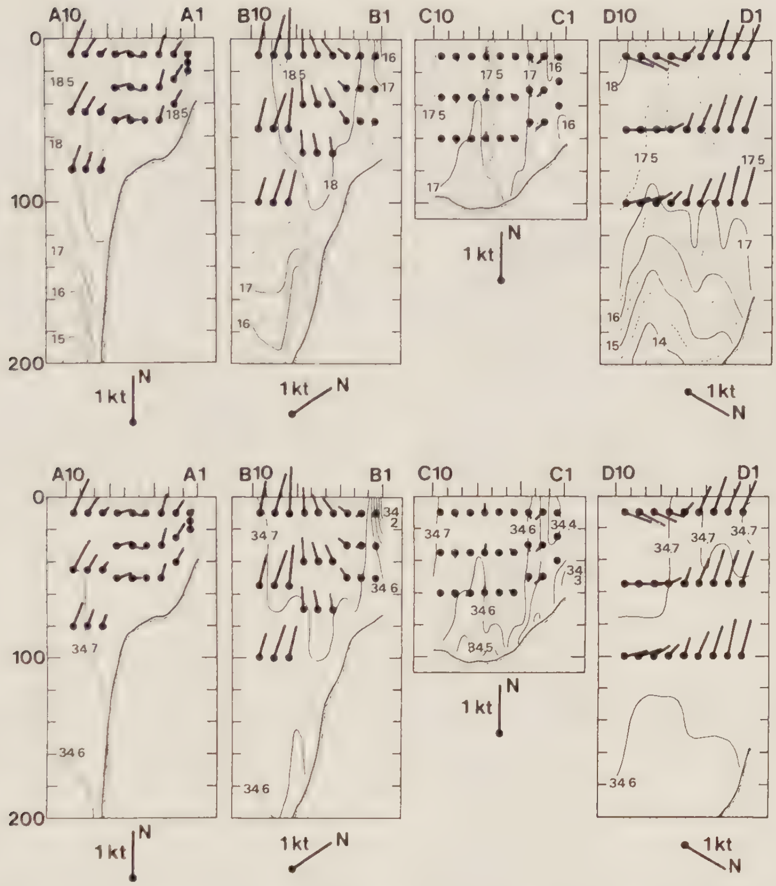


Fig. 3. Temperature (upper panels) and salinity (lower panels) sections with the diurnally averaged flow vectors at three depths in January 1994.
Length and direction of sticks indicate velocity and direction of the diurnally averaged flows, respectively. Northerly direction and sticks's length equivalent to 1 kt are shown below each panel.

Fig. 3 に CTD による各定線での水温・塩分分布を示した．区間 B1－B3および C2－C4 では，水温および塩分のフロントが形成されており，フロントより東側では低水温・低塩分であり，西側では高水温・高塩分であった．さらにそのフロントを境に日周平均流が変化しており，フロント付近では南向きの流れが観測された．九州西岸域では一般に五島側（沖合）よりも九州側（沿岸）の塩分が低いことが報告されており（小笹，1975，中村，1990），本調査の結果もこれと一致している．一方，定線 A と D の100m以浅は34.6以上の高塩分水に占められており，水温・塩分とも明瞭なフロントは観測されなかった．各定線とも海面から100m深付近までの水温・塩分の変化は小さく，各水深層（三層）の日周平均流は，どの層とも10m深の層の流向・流速と概ね一致した．

2） 魚群分布と水塊構造との関係

1994年1月に長崎県沿岸の中小型まき網で最も多く

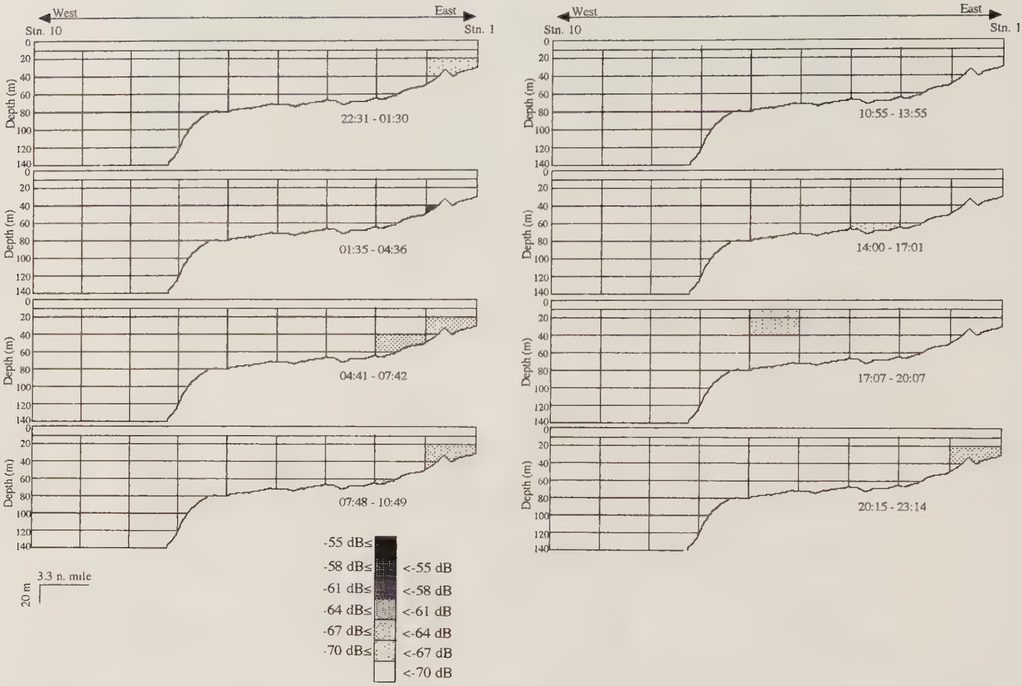


Fig. 4–1. Vertical and horizontal distribution of the Sv value on transect A.

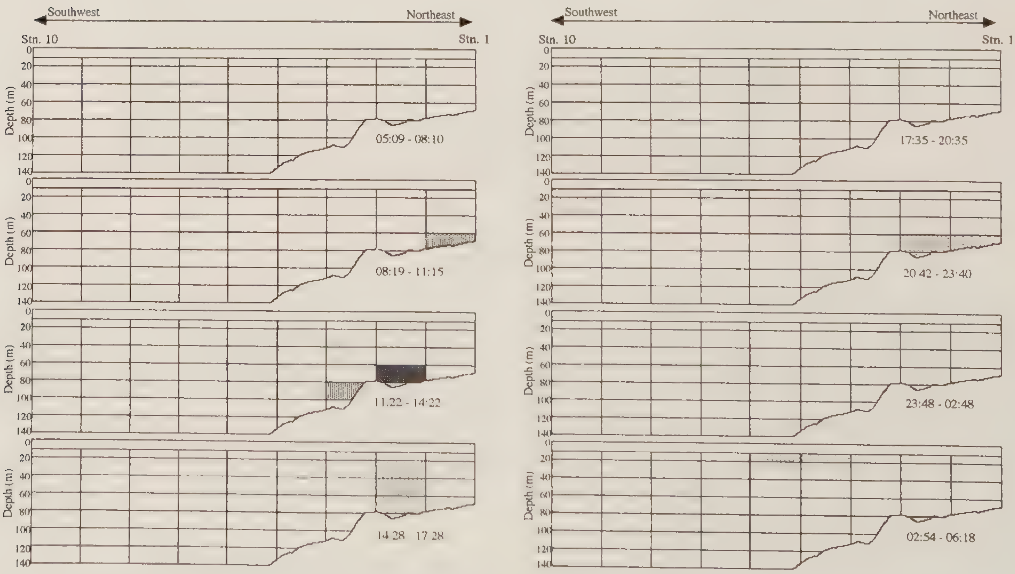


Fig. 4 2. Vertical and horizontal distribution of the Sv value on transect B.

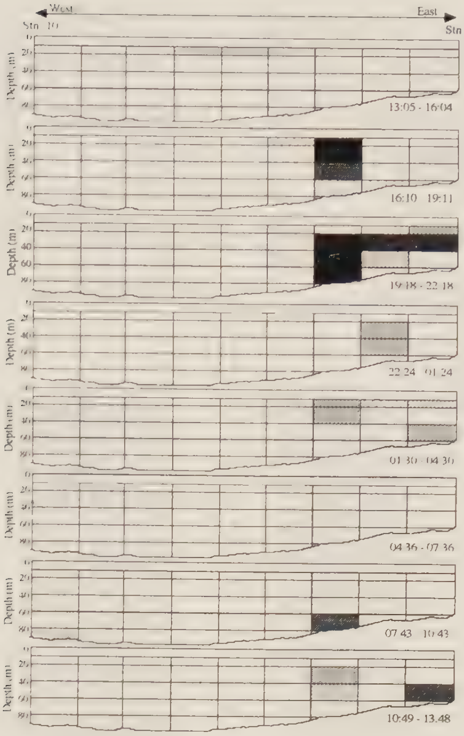


Fig. 4-3. Vertical and horizontal distribution of the Sv value on transect C.



Fig. 4-4. Vertical and horizontal distribution of the Sv value on transect D.

漁獲されたのは，マイワシ（73.0%）であり次いでマアジ（14.6%），マサバ（8.6%），カタクチイワシ（2.7%），そしてウルメイワシ（1.0%）であった（農林水産省長崎統計事務所）．したがって，本研究の魚群探知機で捉えたものの大部分はマイワシである可能性が高い．

Fig. 4 に定線 A，B，C，D における 8 回の水平―鉛直的な Sv 値の分布を示した．定線 A では，定線の東側に魚群反応が現れたもののその値は低かった．一方，定線 B および C においては，定線の東側に強い反応が観察され，とりわけ定線 C では Sv 値が－55dB 以上の濃密な魚群が観測された．魚群反応が強く現れたのは定線 B および C ともフロント付近（図 5-2）に限られていた．

3) 魚群の日周行動

Fig. 5 に，8 回の体積後方散乱係数（*sv* 値）を平均し，この値で標準化したときの表層（10～20 m），中層

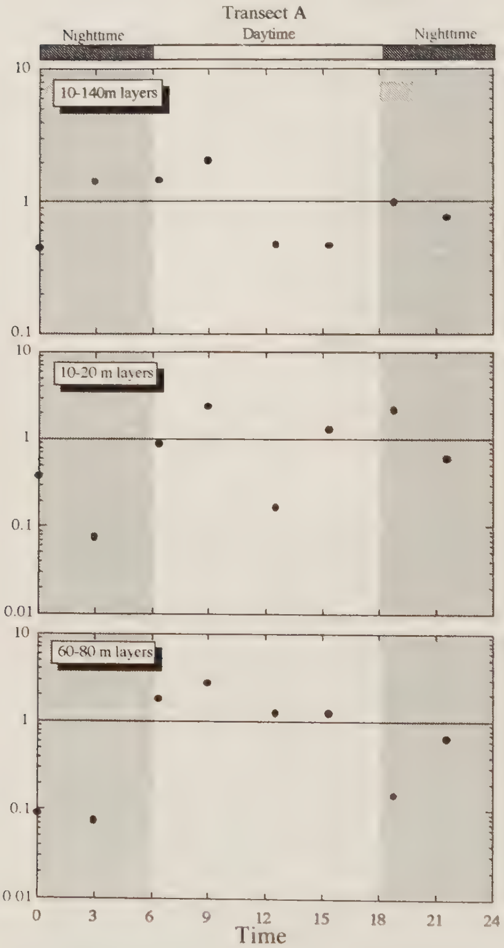


Fig. 5-1. Diurnal variations of the *sv* values at surface (10 to 20 m layers), midwater (60 to 80 m layers) and whole layers (10 to 140 m layers) on transect A. Averaged value from 8 data is set as 1.

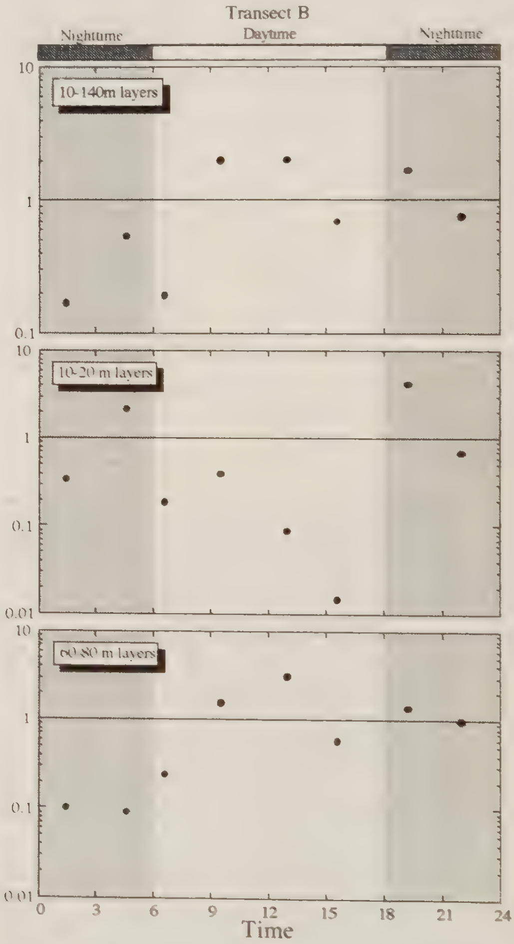


Fig. 5-2. Diurnal variations of the *sv* values at surface (10 to 20 m layers), midwater (60 to 80 m layers) and whole layers (10 to 140 m layers) on transect B. Averaged value from 8 data is set as 1.

[illegible]

本研究の結果、約1日で同一定線を観測しても、[illegible]

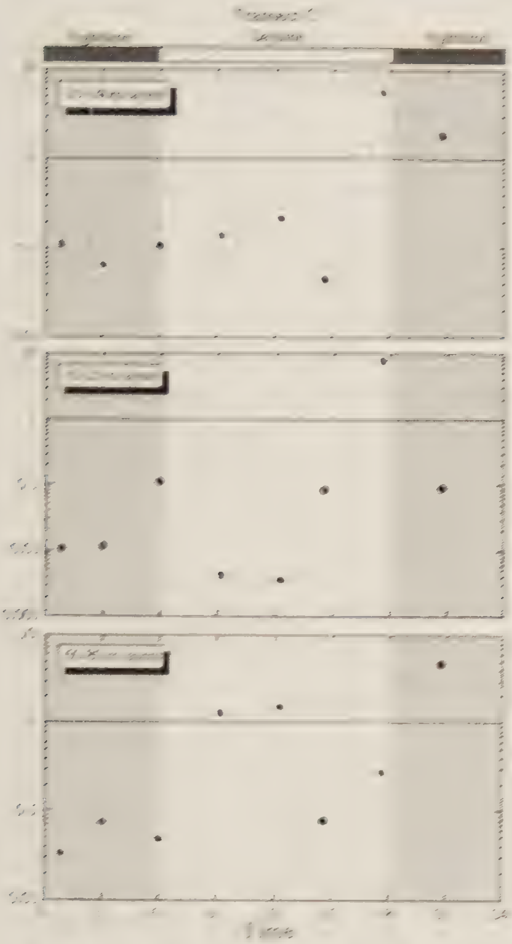


Fig. 5-3 [illegible]

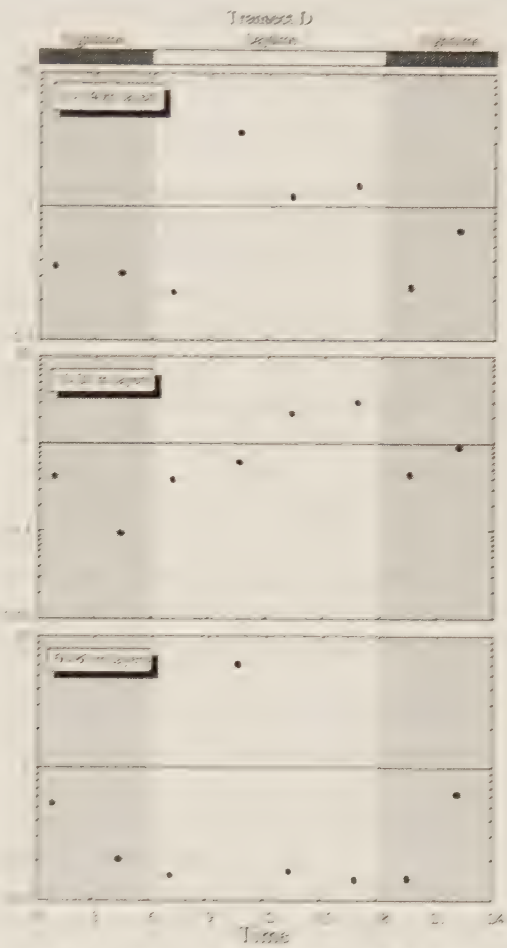


Fig. 5-4 Diurnal variations of [illegible] at surface [illegible] layers), [illegible] layers), and [illegible] m layers) on transect D. (averaged value from 8 [illegible])

考　　察

辻田（1954）は五島南方から天草沖の海域における流況の一般的な模式図として時計回りの流れを示している．ところが，本研究では反時計回りの流れが観察され，辻田（1954）の示した模式図とは逆であった．このことに関して，永谷ら（1994）は1994年1月に甑海峡で投入した漂流ハガキ調査が北方向（牛深市など）へ漂着したのに対し，1995，1996年1月に実施した同様の調査では逆に南東（坊津）へ漂着したことを報告している．また本調査の約2カ月後に観測線Aで行った ADCP による4往復調査では南向きの流れが観察されており（中川ら，1996），本調査で見られたように九州西岸沿いに北向きの流れが生じることは比較的少ない可能性がある．また，漁業情報サービスセンター発行の1994年1月の表面水温の分布をみると，1月4日〜10日には20℃等温線は甑島の南部から離れていたが，11日〜17日および18日〜24日と経過するにしたがって，20℃等温線が甑島に接近する様子が観察されている．このことから，本研究で観測した北向きの流れは，黒潮の一部の流れが北偏し，鹿児島県西岸から向きを北に変えたものと考えられる．なお，観測線Eでみられるトカラ海域から東へ向かう流れは，いわゆる大隅海流（宮地，1991）であると思われる．

水温や塩分などのフロントに魚群が滞留することは古くから報告されており（北原，1918；宇田，1960），「北原の法則」と呼ばれる．その要因として，1）物理的要因（水温や塩分勾配），2）生物的要因（餌生物の存在）の二つに大別される（松村，1984）．フロント域の東側に分布する九州西岸沿岸水は，その西側に分布する対馬暖流系水よりも高いクロロフィルaと高い動物プランクトンの現存量を有している（小笹，1975）ので，今回の観測においてフロント域を中心に魚群が滞留していたのは，沿岸域に高密度に分布する餌生物の影響（生物的要因）を受けた可能性が考えられる．また，仮に今回観測した魚群がマイワシであったとすると，産卵のためにフロント域に形成される南下流を利用して本調査海域よりも北から順次来遊した可能性もある．いずれにせよ，本研究でフロント域を中心に魚群が分布することが明らかになったので，フロントの季節的な変化と，それが魚群の分布・移動に及ぼす物理・生物的な影響を捉えることができれば，音響学的に現存量を推定する際の調査設計の重要な情報となる．

1日のうちに同一定線を調査したにも関わらず，現存量推定値（体積後方散乱係数）は大きく変動した．これまでの研究報告では，音響学的手法による現存量推定値の昼夜での比較では，昼が高いとするもの（Aglen, 1983；Freon et al. 1996）と夜が高いとするもの（Appenzellar and Leggett, 1992）がある．また Freon et al.（1993）は，昼夜それぞれに過小評価の可能性のあることを指摘し，音響学的に現存量を推定する際には調査の時間帯に注意しなければならないことを指摘している．

日本周辺での音響調査では，本田（1994）は北海道道東のサンマの現存量を推定し，昼間のみの体積後方散乱強度を用いて推測した方がよいことを指摘した．東シナ海のカタクチイワシも昼間のみの体積後方散乱強度を用いた方がよいとされる（Ohshimo, 1996）．それは，夜間に浮魚類が表層近くまで浮き上がることにより，近距離干渉（Maclennan and Simmonds, 1992）や，船底に取りつけたトランスデューサーよりも上に魚が分布することによって計測できなくなることによる影響が指摘されているからである（Aglen, 1994）．ただし，太平洋におけるマサバでは，夜間に層状になることは一致するものの，夜間の魚群の遊泳水深が昼間よりも深くなることが観察されている（本城，1977）．このような場合，コンパクトに集群した時間帯（昼間）よりも，層状に広く分布する夜間のほうがより正確な現存量推定ができる可能性がある．したがって，今後は昼夜の魚の集群行動の特徴に注意しながら音響調査を行う必要がある．

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Developmental and Comparative Morphology of Beryciform Larvae (Teleostei: Acanthomorpha), with Comments on Trachichthyoid Relationships

Yoshinobu Konishi

ABSTRACT

The morphological development of nine beryciform larvae, *Beryx* sp. in the Berycidae, *Anoplogaster cornuta* in the Anoplogastridae, *Diretmoides pauciradiatus* and *Diretmichthys parini* in the Diretmidae, *Anomalops katoptron* in the Anomalopidae, *Monocentris japonicus* in the Monocentridae, *Aulotrachichthys* sp., *Hoplostethus* sp. and *Gephyroberyx japonicus* in the Trachichthyidae, and larval polymixiiform, *Polymixia* sp. in the Polymixiidae, is described and illustrated based on larval specimens collected mostly from the western North Pacific. The striking characters shared by these nine beryciform and polymixiiform larvae are well developed head ornamentation with bony ridges and spines. The head spination is different in arrangement and configuration among larvae of the ten species. The beryciform larvae except *Beryx* are also characterized by having additional body ornamentation that may include spinous scales, and spinules on the fin and branchiostegal rays. Other features, such as body shape, anus position, prolonged fin rays, abdominal scutes, hyoid barbels, incipient luminous organs, and pigmentation on the body and pelvic fin are useful for identification of the postflexion larvae of the ten species.

Cladistic analysis of relationships among the Anoplogastridae, Diretmidae, Anomalopidae, Monocentridae, and Trachichthyidae using larval and some adult characters corroborates hypotheses based only on adult characters that these five families are a monophyletic assemblage, anoplogastrids and diretmids are sister groups, and the Trachichthyoidei (anomalopids+monocentrids+trachichthyids) are monophyletic. The analysis also suggests that anomalopids and monocentrids are sister taxa, and the Trachichthyidae are paraphyletic. To clarify the interrelationships among trachichthyids, more complete ontogenetic series of their larvae are needed.

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CONTENTS

INTRODUCTION

Systematic investigations of living beryciform fishes were made by Greenwood *et al.* (1966), Woods and Sonoda (1973), Zehren (1979), Johnson and Patterson (1993) and Moore (1993). In their studies, five families, Anomalopidae, Anoplogastridae, Diretmidae, Monocentridae and Trachichthyidae are members of their Beryciformes or the related order Trachichthyiformes of Moore (1993). However, treatment of the Polymixiidae, Stephanoberycidae, Melamphaidae, Gibberichthyidae and related groups is inconsistent among their works: Greenwood *et al.* (1966) and Woods and Sonoda (1973) placed the Polymixiidae in their Beryciformes, but Zehren (1979), Johnson and Patterson (1993) and Moore (1993) removed the family from the order; the Stephanoberycidae, Melamphaidae, Gibberichthyidae and related groups are included in the Beryciformes of Greenwood *et al.* (1966), Zehren (1979) and Moore (1993), but are excluded from the order by Woods and Sonoda (1973), and Johnson and Patterson (1993). The classification of the Berycidae and Holocentridae differs between two recent works; Johnson and Patterson (1993) placed these two families in the Beryciformes, but Moore (1993) removed them from his Trachichthyiformes (berycoids plus stephanoberycoids), believing them to be more closely related to percoids.

Keene and Tighe (1984) reviewed the larvae of the following Beryciformes: *Anoplogaster cornuta* in the Anoplogastridae; *Diretmus argenteus, Diretmoides pauciradiatus* and *D. parini* (larvae described by Post, 1976; Post and Quero, 1981) in the Diretmidae; Gibberichthyidae (de Sylva and Eschmeyer, 1977); Holocentridae (McKenney, 1959; Jones and Kumaran, 1962); Melamphaidae (Ebeling, 1962); *Korsogaster nanus* (Parr, 1933; Johnson, 1970; Baldwin and Johnson (1995) assigned as *Hoplostethus* spp.) and *Optivus elongatus*? (Crossland, 1981) in the Trachichthyidae. After their reviews, larvae of additional nine genera in five families were described and illustrated: *Beryx splendens, B. decadactylus* (Okiyama, 1988a; Mundy, 1990) and *Centroberyx affinis* (Miskiewicz *et al.*, 1998) in the Berycidae; *Monocentris japonicus* (Okiyama, 1988b) in the Monocentridae; *Gephyroberyx japonicus* (Konishi, 1988a), *Aulotrachichthys* and *Paratrachichthys* (Jordan and Bruce, 1993) in the Trachichthyidae; *Anomalops katoptron* (Colin, 1989; Konishi and Okiyama, 1997) and *Kryptophanaron alfredi* (Baldwin and Johnson, 1995) in the Anomalopidae; and *Acanthochaenus luetkeni* (Kotlyar and Evseyenko, 1989) in the Stephanoberycidae. Recently, Baldwin and Johnson (1995) compared larval morphology among the Beryciformes of Johnson and Patterson (1993). They revealed support for Johnson and Patterson's treatment of the Berycidae, and provided corroborative evidence

for the monophyly of the Anoplogastridae+Diretmidae+Anomalopidae+Trachichthyidae+Monocentridae, a sister-group relationship between diretmids and anoplogastrids, and the monophyly of anomalopids+monocentrids+trachichthyids (trachichthyoids of Johnson and Rosenblatt, 1988). They also noted that larval characters appear to provide no support for a previously proposed relationship between monocentrids and trachichthyids (Zehren, 1979; Moore, 1993). Further, their work addressed the similarity of larval head spination between beryciforms and polymixiiforms, which are not thought to be closely related at present.

Morphological descriptions of all beryciform larvae except those of three diretmids (Post and Quero, 1981), three berycids (Mundy, 1990; Miskiewicz *et al.*, 1998) and three trachichthyids (Jordan and Bruce, 1993) were made with few or a single specimen. There is thus little information about larvae of many Beryciformes and Polymixiiformes, and larvae of some species are unknown.

The purposes of present paper are to describe and illustrate larvae of nine species of the Beryciformes (Johnson and Patterson, 1993): *Beryx* sp. in the Berycidae, *Anoplogaster cornuta* in the Anoplogastridae, *Diretmoides pauciradiatus* and *Diretmichthys parini* in the Diretmidae, *Anomalops katoptron* in the Anomalopidae, *Monocentris japonicus* in the Monocentridae, and *Aulotrachichthys* sp., *Hoplostethus* sp. and *Gephyroberyx japonicus* in the Trachichthyidae. Larvae of the Polymixiiformes, *Polymixia* sp. in the Polymixiidae also are described, and cladistic relationships within the Trachichthyoidei (Johnson and Rosenblatt, 1988) are discussed based on the derived characters of beryciform larvae and adults examined in this study and the characters obtained from the literature.

Most parts of the descriptions of four trachichthyoid larvae and the trachichthyoid relationships in this study have already been presented by Konishi and Okiyama (1997).

MATERIALS AND METHODS

Identification of larval specimens is by the series method using observations of body form, fin-ray counts, pigmentation and head spination, and the literature previously described in the introduction. Larvae were measured to nearest 0.1 mm under a Nikon (SMZ-10) binocular microscope with a Kogaku measuring apparatus. Measurements are as defined by Leis and Rennis (1983). Notochord length (NL) was measured in preflexion and flexion specimens, standard length (SL) in postflexion specimens. Drawings were made with the aid of a camera lucida. Examination of body ornamentation in the form of spinous elements was facilitated by clearing and staining selected specimens, and with the scanning electron

microscope (SEM). Further, ornamentation on the exposed head bones, fin and branchiostegal rays of adults was examined to determine how much of the larval ornamentation is retained in adults and if adults exhibit spination that is lacking in larvae.

A data matrix was constructed and analyzed on PAUP 3.1 (Swofford, 1993) using the general heuristic search to obtain a cladogram of hypothesized relationships within the Trachichthyoidei.

Larval materials described and illustrated in this study are listed below. "CS" and "SM" in parentheses indicate a cleared and stained specimen, and a specimen observed with SEM, respectively. Institutional abbreviations follow Leviton *et al.* (1985); AMS: Australian Museum; BSKU: Department of Biology, Kochi University; HUMZ: Laboratory of Marine Zoology, Hokkaido University. Berycidae.–*Beryx* sp. (5.4 mm SL: 12 Sept., 1986, 24°48.6′ N, 123°17.5′ E; 6.7 mm, 7.4 mm SL: 12 Sept., 1986, 24°47.8′ N, 123°17.8′ E; 8.0 mm (SM) SL: 13 Sept., 1986, 24°47.1′ N, 123°11.3′ E; 9.0 mm SL: 12 Sept., 1986, 24°47.3′ N, 123°14.0′ E; 11.1 mm (CS) SL: 12 Sept., 1986, 24°46.6′ N, 123°18.5′ E). Anoplogastridae.–*Anoplogaster cornuta* AMS I.29352–013 (3.9 mm NL); (4.7 mm, 5.7 mm (SM) SL: 28 Feb., 1973, 24°30.3′ N, 127°11.7′ E; 9.1 mm SL: 26–27 Feb., 1973, 22°01.9′ N, 128°48.7′ E; 15.7 mm (CS) SL: 12 Sept., 1957, ca 30° S, ca 131° W). Diretmidae.–*Diretmoides pauciradiatus* (4.3 mm SL: 13 Sept., 1986, 24°45.1′ N, 123°12.3′ E; 7.6 mm (CS) SL: 13 Sept., 1986, 24°47.0′ N, 123°13.1′ E); *Diretmichthys parini* (3.2 mm NL: 17 Jan., 1975, 24°05.0′ N, 128°44.2′ E; 6.0 mm NL: 4 Feb., 1983, 32°25.2′ N, 133°51.8′ E; 6.4 mm (SM) SL: 28 Feb., 1973, 24°30.3′ N, 127°11.7′ E; 8.8 mm SL: 27 Feb., 1973, 23°23.8′ N, 127°54.3′ E). Anomalopidae.–*Anomalops katoptron* (4.1 mm NL: 11 Sept., 1986, 24°02.0′ N, 122°20.6′ E; 5.8 mm (CS) SL: 12 Sept., 1986, 24°46.5′ N, 123°14.8′ E; 5.8 mm (SM) SL: 11–12 Sept., 1986, 24°02.0′ N, 122°20.6′ E). Monocentridae.–*Monocentris japonicus* (5.7 mm (SM) SL: 24 Oct., 1977, Tosa Bay, Japan; 5.8 mm SL: Nov., 1968, the Kii Straits, Japan; 8.5 mm (CS) SL: 15 Nov., ?, the Kii Straits, Japan). Trachichthyidae.–*Aulotrachi-chthys* sp. (4.6 mm NL: 6 Mar., 1993, 32°15.0′ N, 129°45.0′ E; 7.4 mm (CS) SL: 16 May, 1988, 35°00.0′ N, 150°00.2′ E; 7.6 mm SL: 6 June, 1988, 38°30.7′ N, 144°57.8′ E; 7.7 mm, 9.7 mm SL: 2 June, 1988, 35°31.1′ N, 144°58.1′ E; 10.9 mm SL: 11 Sept., 1989, 35°10′ N, 139°24′ E); *Hoplostethus* sp. (5.4 mm NL: 10 Jan., 1979, 30°20.1′ N, 131°56.7′ E; 9.6 mm (SM) SL: 20 Dec., 1979, 31°57.1′ N, 133°39.5′ E; 10.7 mm (CS) SL: 19 Dec., 1978, 30°26.3′ N, 135°00.1′ E); *Gephyroberyx japonicus* (4.5 mm NL: 10 Feb., 1986, 32°30.3′ N, 134°20.3′ E; 4.6 mm SL: 8 Mar., 1973, 20°58.0′ N, 120°20.0′ E; 11.0 mm (CS) SL: 4 Feb., 1983, 32°25.2′ N, 133°51.8′ E); *Gephyroberyx* sp. AMS I.32786–006 (3.4 mm NL). Polymixiidae.–*Polymixia* sp. (3.9 mm SL: 5 July, 1984, 27°54.3′ N, 127°39.0′ E; 6.0 mm (SM) SL: 7 Sept., 1986, 23°59.6′ N, 124°45.1′

E; 10.0 mm (CS) SL: 6 Sept., 1986, 23°00.1′ N, 127°09.9′ E). Above larval specimens except the Australian Museum's (AMS) ones are deposited in the author's Institute, Seikai National Fisheries Research Institute. Adult material examined is below. *Beryx splendens*: BSKU23211.*B.decadactylus*: BSKU36926. *Centroberyxlineatus* (=*druzhinini*): BSKU 2344. *Anoplogaster cornuta*: HUMZ 77473. *Diretmoides pauciradiatus*: BSKU 23107. *Anomalops katoptron*: BSKU 8879. *Monocentris japonicus*: BSKU 8844. *Paratrachichthys* (=*Aulotrachichthys*) *prosthemius*: BSKU 38327. *Hoplostethus japonicus*: BSKU 39856. *Gephyroberyx japonicus*: BSKU 7237. *Paratrachichthys* sp.: AMS I.35492-001. *Optivus* sp.: AMS I.30408-007.

Family BERYCIDAE

The Family Berycidae (Alfonsinos) contains two genera, *Beryx* and *Centroberyx*, with about nine species in the western and central Pacific, Indian and Atlantic (Nelson, 1994). *Beryx* and *Centroberyx* are similar in general appearance, but are separated mainly by presence or absence of a lachrymal spine, and meristic characters, such as anal-, pectoral- and pelvic-fin rays, and lateral-line scales (Woods and Sonoda, 1973). Four berycids, *B. splendens, B. decadactylus, B. mollis* and *C. druzhinini*, occur in Japan. *B. splendens* is different from *B. decadactylus* in having fewer dorsal-fin rays (13-15 vs. 18-20). *B. mollis*, described as a new species by Abe (1959) based on specimens from Sagami Bay, Japan, usually has been recognized as a synonym of *B. splendens* (Hayashi, 1993a), but the former species is distinguished from the latter in having fewer dorsal-fin rays (12-13 vs. 13-15), fewer pyloric caeca (15-19 vs. 27-36), and higher values of three body proportions: the ratios of body depth to body length (39.0-43.2% vs. 33.9-38.4%), eye diameter to body length (14.0-15.7% vs. 10.6-13.5%), length of the longest pelvic-fin ray to body length (24.1-27.4% vs. 19.8-24.3%) (T. Yoshino, University of the Ryukyus, pers. comm., in Hayashi, 1993a).

Some information about the early life stages of *B. splendens* is known: fertilized eggs and reared yolk-sac larvae (Onishi, 1966; 1968); a wild-caught postflexion larva of 10.7 mm SL (Okiyama, 1988a). Mundy (1990) described and illustrated larvae and juveniles of two berycids, *B. splendens* and *B. decadactylus*, based on a series of specimens, and reviewed their characters pertinent to phylogeny of the Beryciformes including the Melamphaidae. Very recently, Miskiewicz *et al.* (1998) described and illustrated larvae and juveniles of *Centroberyx affinis*.

In this study, larvae of *Beryx* sp., which are assigned as *B. splendens* or *B. mollis* on the basis of fin-ray counts, are described and illustrated based on six specimens from 5.4 mm to 11.1 mm SL.

Beryx sp.
Figures 1, 2

General Morphology

Early postflexion larvae have a slender and quite compressed body, but they become slightly deeper with growth (Fig. 1). The body depths of postflexion larvae from 5.4 mm to 11.1 mm SL are between 30.7 and 41.1% SL. The head is moderate, and its length occupies about one-third body length, becoming relatively shorter with development due to extension of the tail. The eye occupies about 30% of the head length, and is round. The snout is moderately long (26 to 34% of head length), and the rostral cartilage conspicuously projects at the snout. The superior mouth is large and oblique, and the posterior margin of the upper jaw extends beyond the center of the eye. In the 5.4 mm SL larva, there are about ten tiny teeth on the entire premaxilla, and three small teeth on the anterior portion of the dentary. The number of teeth on both jaws increases with development; the 11.1 mm larva has about fifteen teeth on the premaxilla, and several on the dentary. The anus is near mid body in the 5.4 mm larva, but the distance from the tip of the snout to the anus becomes relatively shorter with growth.

Scales begin to form between 7.4 mm and 9.0 mm SL; in the 9.0 mm larva, the body except the region around the pectoral fin is covered with scales, and the adult complement of 63 lateral-line scales is countable. Unlike scales of other beryciform larvae, such as the Anoplogastridae, Diretmidae, Anomalopidae, Monocentridae and Trachichthyidae, larval scales of *Beryx* do not have erect spinules and are superficially smooth.

Fins and Meristics

In the smallest postflexion larva of 5.4 mm SL examined, all fins are forming, and a remnant of the finfold is present above the caudal peduncle. The dorsal fin (II, 15) is located at mid body, and its full complement (IV, 13) is present in the 9.0 mm larva. Although dorsal-fin rays of all specimens examined are damaged distally, the anteriormost soft ray is believed to be elongated notably: the first soft ray of *Beryx* in larval and juvenile stages is over twice the body length (Okiyama, 1988a; Mundy, 1990). This character is retained by the young stage at least to 170 mm SL (Abe, 1969; Fourmanoir, 1976; Krefft, 1976). Larval *Centroberyx affinis* have a usual dorsal fin without any notably elongate rays (Miskiewicz *et al.*, 1998). Dorsal-fin rays of *Beryx* sp. bear a posteriorly projecting, hook-shaped, tiny spine at both sides of the base; the 5.4 mm larva has the spine on the first seven of 17 rays, and the 11.1 mm larva has it on all rays. The anterior spines are larger in

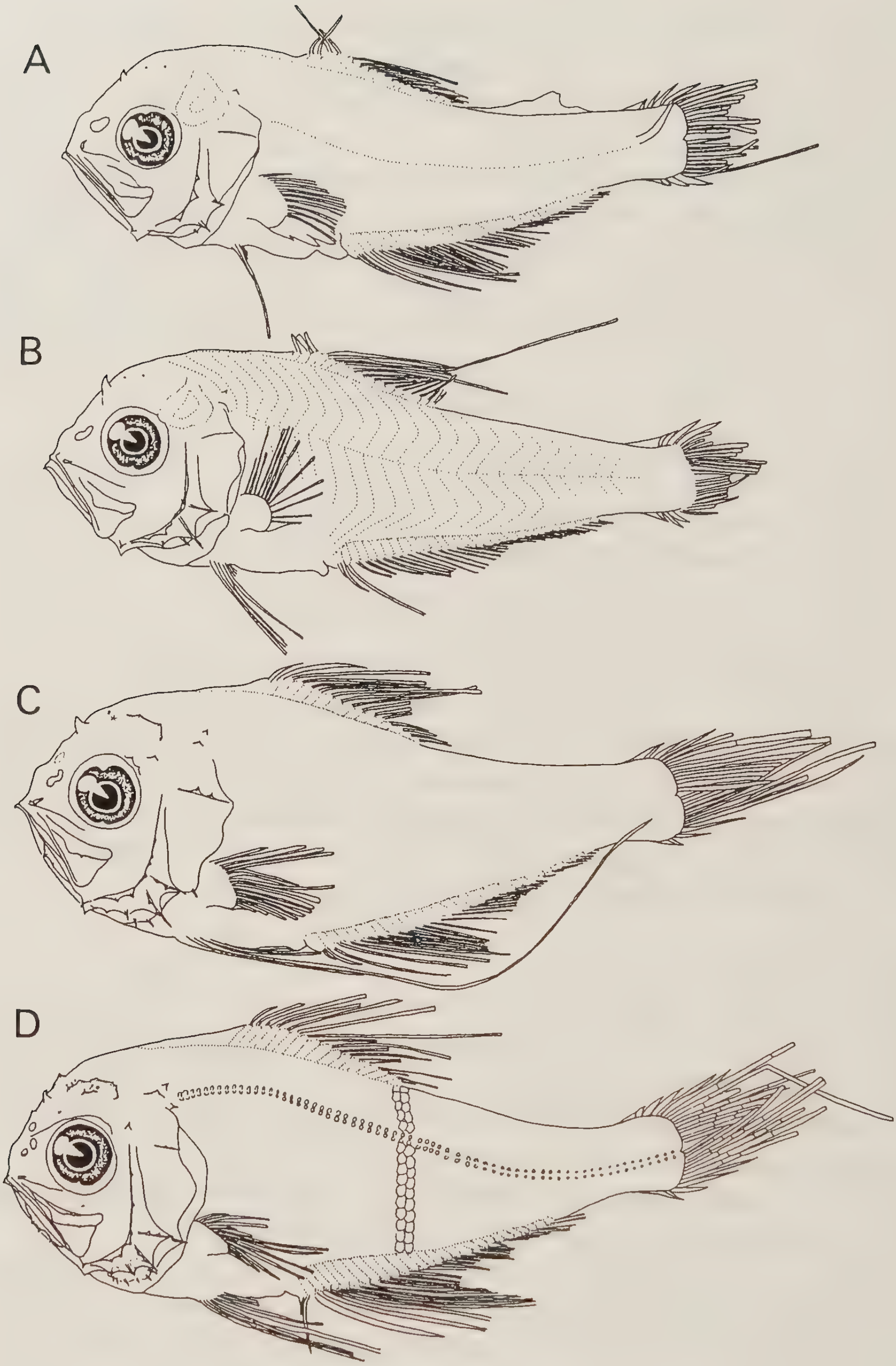


Fig. 1. Larvae of *Beryx* sp.. A) 5.4 mm SL; B) 6.7 mm SL; C) 7.4 mm SL; D) 11.1 mm SL.

size than the posterior ones. The anal-fin base is relatively long, as in the Pempheridae. The full complement of fin rays (IV, 30) is present in the 9.0 mm larva. A hook-like spine bilaterally occurs on the each base of the first eight rays of the 5.4 mm specimen, and the first 21 rays of the 11.1 mm larva. The adult complement of principal caudal-fin rays (10+9) is present in the 5.4 mm larva. The 7.4 mm larva has a full complement of the procurrent spines: 5 in the upper side, 4 in the lower side. Most of the pelvic-fin rays of all specimens examined are damaged distally. In the 6.7 mm and 9.0 mm larvae, the second pelvic ray is very prolonged, its length in the latter about 80% SL. Yolk-sac larvae of *B. splendens* have a membranous pelvic fin (Onishi, 1966; Mundy, 1990), and thus the fin is precocious. But the fin develops slowly, the largest larva of 11.1 mm studied having one spine and 8 soft rays, whereas the complement is I, 9–11. Larval *Centroberyx* also has the early forming pelvic fin, but the longest ray (2nd ray) does not extend beyond the posterior margin of the anal fin (Miskiewicz *et al.*, 1998), and is thus considerably shorter than that of *Beryx*. Seven incipient rays appear dorsally in the pectoral fin of the 5.4 mm larva: rays develop from the dorsal part, and the full complement (16) is present in the 9.0 mm specimen.

The 5.4 mm larva has complete sets of vertebrae (10+14) and branchiostegal rays (8); no spination is present on the branchiostegal rays.

Pigmentation

Although the tip of the notochord, anus and incipient pelvic fin are heavily pigmented in preflexion larvae of 4 days post hatch (Onishi, 1968), pigment of the postflexion larvae examined is very sparse, and is restricted to the head above the eye and on the pelvic fin; on the head, there are two to ten small stellate melanophores and a short line of pigment over the eye; 3 to 15 punctate melanophores are scattered on the first and second rays of the pelvic fin.

Head Spination

Postflexion larvae of *Beryx* develop moderate head spination (Fig. 2). In the 11.1 mm larva cleared and stained, the frontal anterodorsally bears two spines projecting outward. Furthermore, the bone develops two obliquely oriented, nearly parallel, serrate ridges on the posterolateral surface; the upper is longer than the lower. Although the supraorbital ridges of juveniles (approximately 22 mm SL) of *B. splendens* and *B. decadactylus* have some spines (Mundy, 1990), the ridge of the 11.1 mm larva bears no spines. The surface of the frontal over the midbrain is rugose (Appendix Fig. 1). Two characteristic spines occur on the anterior tip of the lachrymal; the posterior spine is large and curved, and extends back-

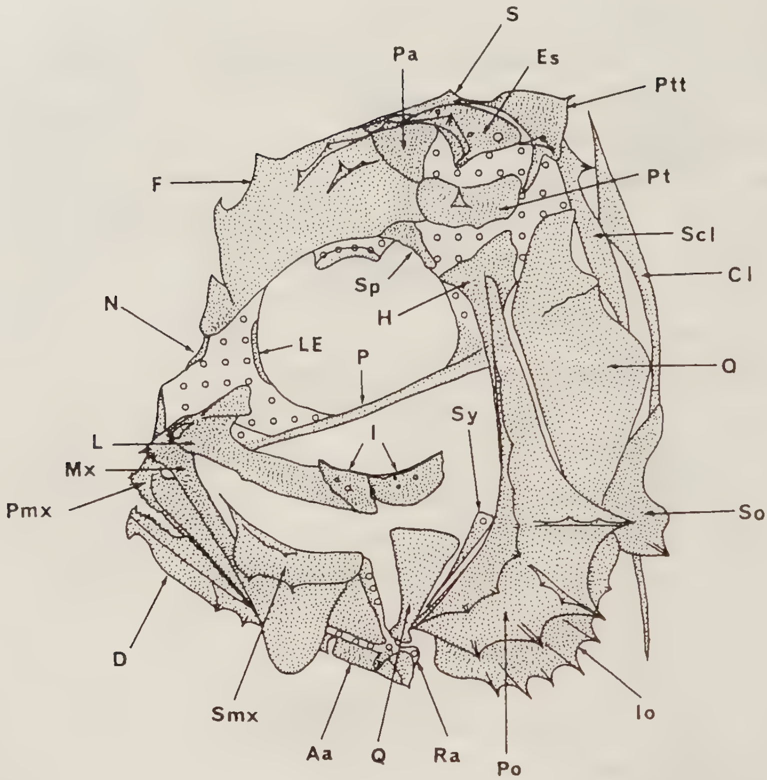


Fig. 2. Head spination of *Beryx* sp. in 11.1 mm SL. Larger stippling in the figure represents cartilage. F–frontal, N–nasal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, S–supraoccipital, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Cl–cleithrum.

ward; the anterior is small, and faces anteroventrally. The first two infraorbitals have a low ridge with serration on the upper margin. The nasal is very small, and has no spination. But, Mundy's (1990) and Baldwin and Johnson's (1995) specimens more than 15 mm SL have the ornamented nasal. A curved, serrate ridge is present on the lateral surface of the extrascapular, and the anterior tip of the ridge joins the upper ridge on the posterolateral surface of the frontal. The parietal partially covered with the extrascapular has no spination. There is a single spine on the lateral surface of the pterotic. Two tiny spines occur on the anterior tip of the maxilla; the spines are lost in the juvenile stage (Mundy, 1990). The supramaxilla bears a serrate ridge on the dorsolateral surface and 3 spines on the ventral

edge. The dentary has three spines on the lower edge. An outward projecting spine appears on the posterolateral surface of the anguloarticular, as in young of *B. decadactylus* (Abe and Maruyama, 1971). The preopercle consists of the dorsal and ventral limbs. A ridge with the equally spaced, small spines lies on the anterolateral surface of the preopercle. On the posteroventral margin of the ventral limb, there are four wide spaced spines, and each spine of the upper two is associated with a serrate ridge on the lateral surface. The interopercle has six spines on the posterior edge. A single spine is present on the posteroventral tip of the subopercle. An obliquely oriented, low, serrate ridge appears on the dorsolateral surface of the opercle. The posttemporal bears a minute spine on the posterodorsal corner, and a ridge with a single spine on the ventral surface. The supracleithrum has a tiny spine near the posttemporal ridge.

Postflexion larvae of *Centroberyx affinis* develop moderate head spination on the most exposed bones, but no outward projecting spines, as seen in larval *Beryx*, occur on the frontal and lachrymal, and the dentary and anguloarticular have no spination (Miskiewicz *et al.*, 1998). In a 29.5 mm SL juvenile of *Centroberyx* sp., which was caught on 30th June 1995 in the Tasman Sea off the coast of Sydney, head spination is extremely similar to or more advanced than that of larval *Beryx* sp. described above; the clearing and staining juvenile possesses no outward projecting spines on the frontal and lachrymal, but develops additional spination on the nasal, sphenotic, maxilla, and 3rd and 4th branchiostegal rays.

Family ANOPLOGASTRIDAE

The Family Anoplogastridae (Fangtooths), consists of a single genus, *Anoplogaster*, with two species, *A. cornuta* and *A. brachycera*. Adults are characterized by fanglike teeth, a small eye and spineless fins (Nelson, 1994). *Anoplogaster brachycera*, which was first described by Kotlyar (1986a) based on juveniles from 20 mm to 60 mm SL, is known only from the tropical West Pacific (Sulu Sea) and Atlantic (Gulf of Mexico and northeast of the Bahamas), but *A. cornuta* has a widespread distribution in the circumtropical sea (Kotlyar, 1986a). In the juvenile stage, *A. brachycera* differs from *A. cornuta* in having fewer rays in the dorsal fin (16–17 vs. 17–19 in *A. cornuta*), and smaller spines on the parietal and the angle of the preopercle (Kotlyar, 1986a).

Description and illustration of larval *A. cornuta* were made by Keene and Tighe (1984), Okiyama and Hirano (1988) and Watson (1996a) based on the flexion and/or postflexion larvae, but preflexion larvae are unknown.

In this study, larval *A. cornuta* identified by dorsal-fin count and collecting

locality are described and illustrated based on the 5 specimens including a preflexion larva and juvenile.

Anoplogaster cornuta

Figures 3, 4

General Morphology

A 3.9 mm NL preflexion larva is moderately deep (body depth at the pectoral-fin base 33.3% NL), but two postflexion larvae of 4.7 mm and 9.1 mm SL are round in shape, their body depths occupying about 74% SL and 53% SL, respectively (Fig. 3). These postflexion larvae have a slightly wide head and trunk with a compressed tail. The head is initially moderate in length, and becomes large with growth (head length 28.2% NL to 37.4% SL). The large eye (54.5% to 41.2% HL) is round. The snout is blunt. The mouth is large and oblique. No teeth appear in the 3.9 mm and 4.7 mm larvae, but the 9.1 mm larva has three tiny teeth on the anterior portion of the dentary. The anus is situated posteriorly just before the origin of the anal fin (preanal length 76.9% NL to 71.4% SL).

No scales cover any region of the body in the 3.9 mm and 4.7 mm specimens. In the 9.1 mm larva, scales with a single, nearly erect spinule are present only on the ventral midline between the isthmus and the base of the pelvic fin. As in diretmid larvae described below, such a localized distribution of scales of larval *Anoplogaster* is unusual among those of beryciform larvae. A 15.7 mm SL juvenile bears spiny scales on the almost entire body including the caudal fin; most scales on the ventral surface of the gut and thorax possess crown-shaped ornamentation with 4 spines, and similar spination with one to four spinules is observed on the other scales; at least 15 remarkably large, pored scales with horizontally parallel, slightly curved, serrate ridges are aligned at intervals on the lateral line from just posterior to the posttemporal to the base of the median rays of the caudal fin.

Fins and Meristics

In the 3.9 mm larva, the pelvic fin is absent, and other fins are membranous. The incipient base of the dorsal fin lies in the posterior region of the dorsal finfold, but that of the anal fin is in place. The 4.7 mm larva is developing all fins except the bud of the pelvic fin under the pectoral-fin base. The large pectoral fin is nearly perpendicular to the lateral axis of the body, the longest ray nearly reaching the dorsal margin of the trunk. Full complements of fin rays are observed in the 9.1 mm larva: dorsal-fin rays (18), anal-fin rays (8), pectoral-fin rays (15), pelvic-fin rays (7), and principal caudal-fin rays (10+9). No spinules



Fig. 3. Larvae of *Anoplogaster cornuta*. A) AMS I.29352-013, 3.9 mm NL; B) 4.7 mm SL; C) 9.1 mm SL.

occur on fin rays of the larva. Most rays of all fins of the 15.7 mm juvenile bear one to five spinules on the lateral surface of the basal one-third, although Baldwin and Johnson's (1995) specimens up to 10.5 mm SL possess such spination only on the dorsal- and anal-fin rays. The largest larva examined as well as an adult *A. cornuta* (HUMZ 77473) have eight branchiostegal rays, none of which has spinules or serration.

Pigmentation

In the 3.9 mm larva, the dorsal to lateral surface of the gut is well pigmented. Pigment occurs over the brain, on the posterodorsal region of the trunk, and around the posteroventral area of the eye and gas bladder. In the 4.7 mm larva, melanophores extensively cover the trunk except its dorsal margin and the ventral side of the gut, and the base of the pectoral fin is pigmented. Additional pigment occurs on the opercular and otic regions, cheek, isthmus and ventral midline before the pelvic-fin base in the 9.1 mm larva.

Head Spination

The 3.9 mm preflexion larva has no spination on the head. The two postflexion larvae of 4.7 mm and 9.1 mm SL are characterized by having a large spine on the parietal, supraorbital and preopercle. These large spines occur initially as a low, triangular, non-serrate spine in a 4.9 mm TL flexion larva (Okiyama and Hirano, 1988). In the 9.1 mm larva examined, the surfaces of the three spines are rugose with serrate and non-serrate ridges; the serrate ridges originate from the top point of each spine, and extend to its basal region radiately (for the parietal, Appendix Fig. 2A). The lengths of the parietal and preopercle spines are 97% and 79% HL, respectively. The following description of head spination on the other bones is made based on a cleared and stained juvenile of 15.7 mm SL (Fig. 4), because the 9.1 mm larva could not be stained. Decalcification may have occured in the specimen during the long preservation of more than 15 years. The frontal is rugose with serrate and non-serrate ridges, which are associated with ridges on the supraorbital. Serrate ridges and/or small spines are present on the lateral surfaces of the lachrymal, infraorbitals, sphenotic and pterotic. The small extrascapular located over the posteroventral area of the parietal has a ridge with three spines on the anterior margin. The supramaxilla is adorned with spiny ridges. Five serrate ridges occur on the ventrolateral surface of the dentary. The anguloarticular is rugose and possesses serrate and non-serrate ridges. Vertically oriented, serrate ridges connected with ridges on the prolonged preopercle spine are present on the lateral surface of the upper limb of the preopercle. The opercle is

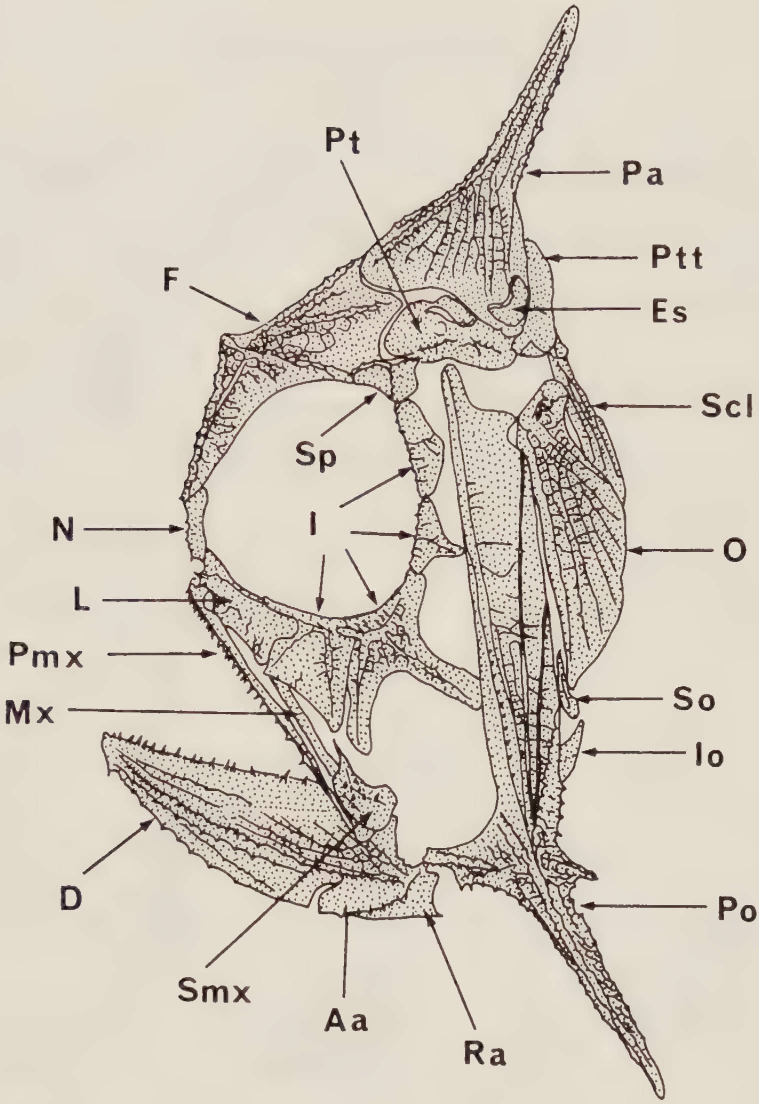


Fig. 4. Head spination of *Anoplogaster cornuta* in 15.7 mm SL. F–frontal, N–nasal, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, Es–extrascapular, Pa–parietal, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum.

rugose with serrate and non-serrate ridges. The small, membranous subopercle has a single, low, non-serrate ridge. The posttemporal bears spiny ridges on the lateral surface. The supracleithrum is rugose with smooth ridges.

Family DIRETMIDAE

The Family Diretmidae (Spinyfins), consists of three genera, *Diretmus, Diretmoides*, and *Diretmichthys*, with four species (Nelson, 1994). *Diretmus* is characterized by the position of the anus placed just before the anal-fin origin, the presence of scutes on the ventral midline anterior to the pelvic fin, and a large number of ridges on the upper third of the opercle, whereas *Diretmoides* has the anus between the pelvic-fin base and the anal-fin origin, no scutes in the thorax, and fewer ridges on the dorsolateral surface of the opercle (Post and Quero, 1981). Kotlyar (1990) placed *Diretmoides parini* (Post and Quero, 1981) in a new, monotypic genus, *Diretmichthys*, which is clearly different from two other genera in having no fusion between the third and fourth hypurals, a higher number of vertebrae, and enlarged spines on the bases of the dorsal- and anal-fin rays. Kotlyar (1987) reported that two diretmids, *Diretmichthys* (as *Diretmoides*) *parini* and *Diretmoides pauciradiatus*, are distributed in Japan and its adjacent waters; *D. parini* is distinguished from *D. pauciradiatus* by the higher numbers of the dorsal-fin rays (26–30 vs. 24–27), anal-fin rays (20–23 vs. 18–21), and vertebrae (30–32 vs. 27–30).

Larval morphology of diretmids was described and illustrated for *Diretmus argenteus*, *Diretmoides pauciradiatus* and *Diretmichthys* (as *Diretmoides*) *parini* by Post (1976), Post and Quero (1981) and Watson (1996b), but their descriptions are too brief to use in a phylogenetic analysis among beryciforms, particularly regarding body oranamentation, and they do not include preflexion larvae. Baldwin and Johnson (1995) tabulated the details of the ornamentation of larval diretmids in comparison of morphology among beryciform larvae.

In this study, development of two diretmids, *D. pauciradiatus* and *D. parini*, identified by fin-ray and vertebral counts, pigmentation and collecting locality, are described and illustrated based on two specimens of *D. pauciradiatus* of 4.3 mm and 7.6 mm SL, and four specimens of *D. parini* of 3.2 mm NL to 8.8 mm SL.

Diretmoides pauciradiatus
Figures 5, 6

General Morphology

Two postflexion larvae of 4.3 mm and 7.6 mm SL (Fig. 5) are rhombic in shape, very deep and quite laterally compressed (body depth at the pectoral-fin base 68% to 74% SL). The body depth of preflexion or flexion larvae unavailable in this study is probably moderate as in preflexion larvae of *D. parini* described

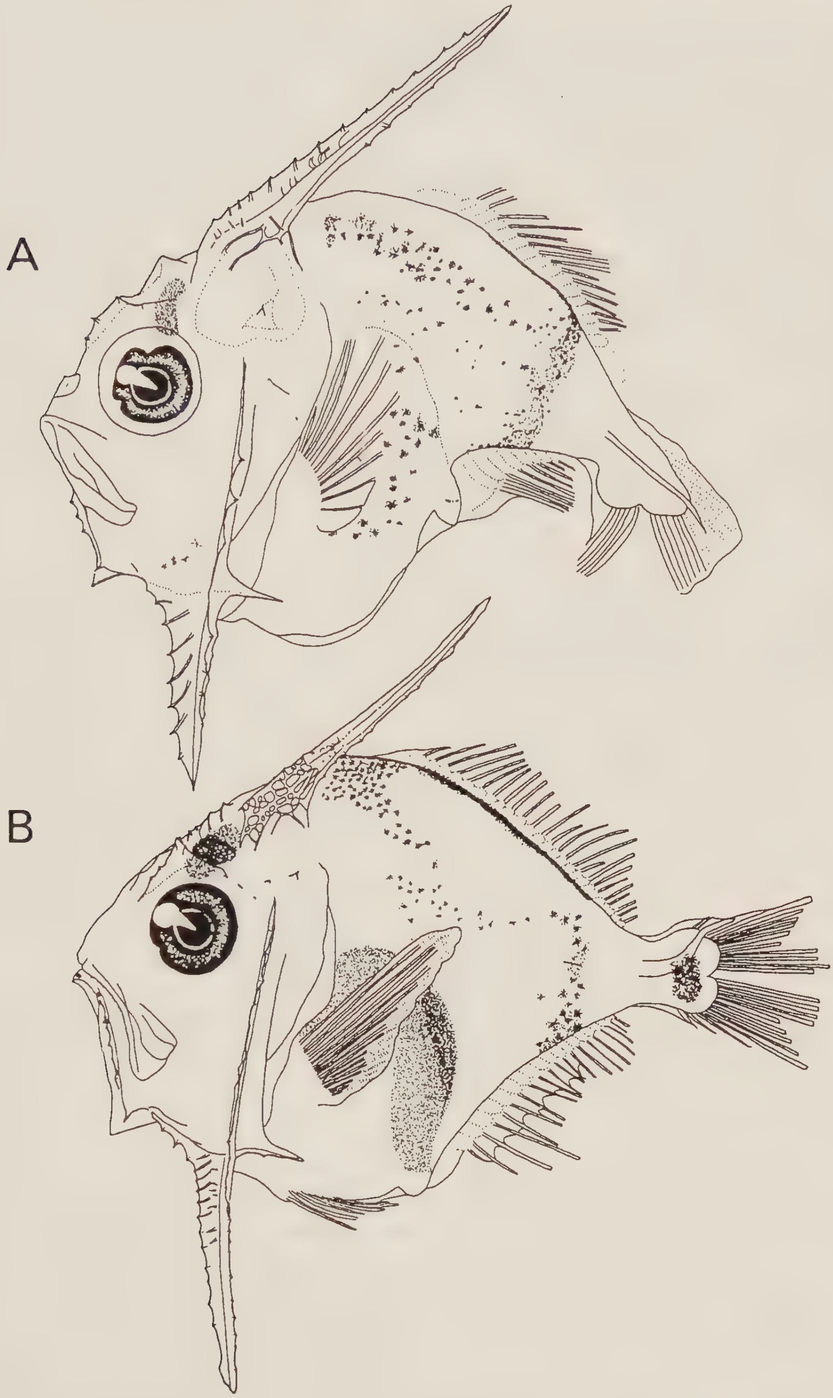


Fig. 5. Larvae of *Diretmoides pauciradiatus*. A) 4.3 mm SL; B) 7.6 mm SL.

below. In the two larvae of *D. pauciradiatus*, the head is large, its length about 39% SL. The eye occupies about 30% HL, and is round. The snout (23% to 33% HL) is blunt. The terminal mouth is oblique and large, its posterior margin reaching the center of the eye. In the 7.6 mm specimen, there are 15 teeth on the anterior two-thirds of the dentary, and about 20 tiny teeth along the entire length of the premaxilla. The gut is coiled. The anus is located near mid body; there is a gap between the anus and the origin of the anal fin in the larger specimen examined. In large larvae of diretmids, except *Diretmus*, the anus is located centrally between the base of the pelvic fin and the origin of the anal fin (Post and Quero, 1981).

Larval *Diretmoides* has spinous scales and scutes only on the ventral midline of the anterior trunk (Post, 1976; Post and Quero, 1981; Baldwin and Johnson, 1995). But neither the scales nor the scutes yet appear in either larva examined.

Fins and Meristics

In the 4.3 mm larva, all fins except the pelvic fin are forming: dorsal-fin rays (15), anal-fin rays (10), pectoral-fin rays (10), and principal caudal-fin rays (6+6). The 7.6 mm larva has a full complement of dorsal-fin rays (25), anal-fin rays (20), pectoral-fin rays (17), pelvic-fin rays (7), and principal caudal-fin rays (10+9). Most rays of the median fins are damaged distally. The pectoral fin is posterodorsally prolonged, its longest ray extending greatly beyond the lateral midline of the body. None of the fin rays are ornamented with spinous elements. But, Baldwin and Johnson (1995) noted that larvae larger than about 15 mm SL have spinules on the lateral surfaces of the dorsal- and anal-fin rays. An adult of *D. pauciradiatus* (BSKU 23107) bears spinules on rays of all fins; spinules on the dorsal-, anal- and pelvic-fin rays are very prominent.

The 7.6 mm larva cleared and stained has 29 vertebrae. There are seven branchiostegal rays without spination.

Pigmentation

Larval *D. pauciradiatus* is more sparsely pigmented than that of *D. parini* described below. The 4.3 mm larva of *D. pauciradiatus* has a line of pigment along the middle portions of the dorsal- and anal-fin bases. A light, narrow pigment band appears vertically between the posterior margins of the two lines of pigments. Melanophores are scattered on the lateral surface of the trunk. Additional pigment occurs on the brain, dentary and base of the ventrally prolonged preopercular spine. In the 7.6 mm larva, pigment along the dorsal-fin base spreads anteriorly to the predosal region, and a conspicuous pigment spot is present on the

caudal–fin base. The dorsal side of the head is pigmented over the brain. There are five stellate melanophores on the dentary.

Head Spination

Prominent head ornamentation of larval diretmids comprises prolonged spines on the parietal and preopercle (Fig. 6). The lengths of the parietal and preopercle spines of larval *D. pauciradiatus* are 112% and 76% HL in the 4.3 mm larva, and 107% and 100% HL in the 7.6 mm larva, respectively. In the larger specimen,

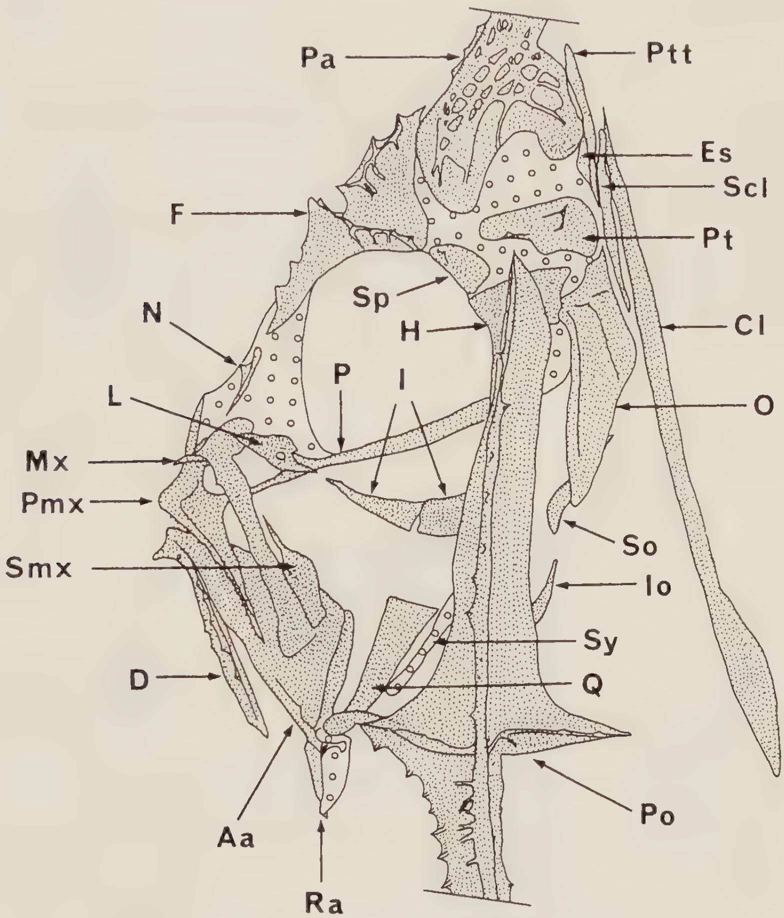


Fig. 6. Head spination of *Diretmoides pauciradiatus* in 7.6 mm SL. Larger stippling in the figure represents cartilage. F–frontal, N–nasal, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Cl–cleithrum.

serrate ridges originating from the top of the parietal spine lie longitudinally along the anterior, posterior, and lateral surfaces of the spine. The base of the parietal spine is rugose due to a web-like arrangement of non-serrate ridges. On the cross-shaped preopercle, a serrate ridge lies from the dorsal to ventral tip of the lateral surface. The ventrally prolonged spine of the preopercle has serrations on the anterior, posterior, and lateral surfaces. At the base of the spine, there is a backward projecting spine, which bears a horizontally oriented, non-serrate ridge on its lateral surface. This ridge extends to the anterior tip of the preopercle. A large, triangular spine with a wide base is conspicuously present on the supraorbital, and is serrated on the upper margin. On the dorsolateral surface of the frontal, there are two ridges nearly in parallel with the dorsal midline of the body. The outer ridge is serrate, and its anterior portion is joined to the inner ridge without serration. Two serrate, parallel ridges are present on the ventral side of the dentary, and a small spine appears on the lowermost tip of the anguloarticular. The opercle bears three non-serrate ridges on the lateral surface. One or two tiny spines are present on the sphenotic and pterotic. No ornamentation appears on the other exposed head bones. Baldwin and Johnson (1995) described spination on the supramaxilla, infraorbitals, nasal, extrascapular and posttemporal in their specimens, and an adult *D. pauciradiatus* (BSKU 23107) possesses further spination on the subopercle and interopercle. The parietal, supraorbital and preopercle spines that are enlarged during the early life stages are ontogenetically lost or reduced.

Diretmichthys parini
Figure 7

General Morphology

Two preflexion larvae of 3.2 mm and 6.0 mm NL (Fig. 7) have a moderately deep body (body depths 31% and 32% NL, respectively). Body size at the beginning of flexion of the notochord is more than 6.0 mm, and thus larger than that of *D. pauciradiatus*. The body of an 8.8 mm SL postflexion larva is deep (64% SL) and laterally compressed. The head is moderate in length (28% NL) in the preflexion larvae, and is large (42% SL) in the postflexion larva. The eye occupies about 35% HL, and is large and round. The snout is blunt and about 25% HL. The mouth is oblique and large, its posterior margin reaching beyond or under the center of the eye. The largest specimen examined has many tiny teeth on the entire length of the premaxilla and dentary. The gut is coiled. Anus position is posterior to mid body in the preflexion larvae, the preanal length about 60% NL. In the 8.8 mm postflexion larva, the anus is located mid way between the pelvic-

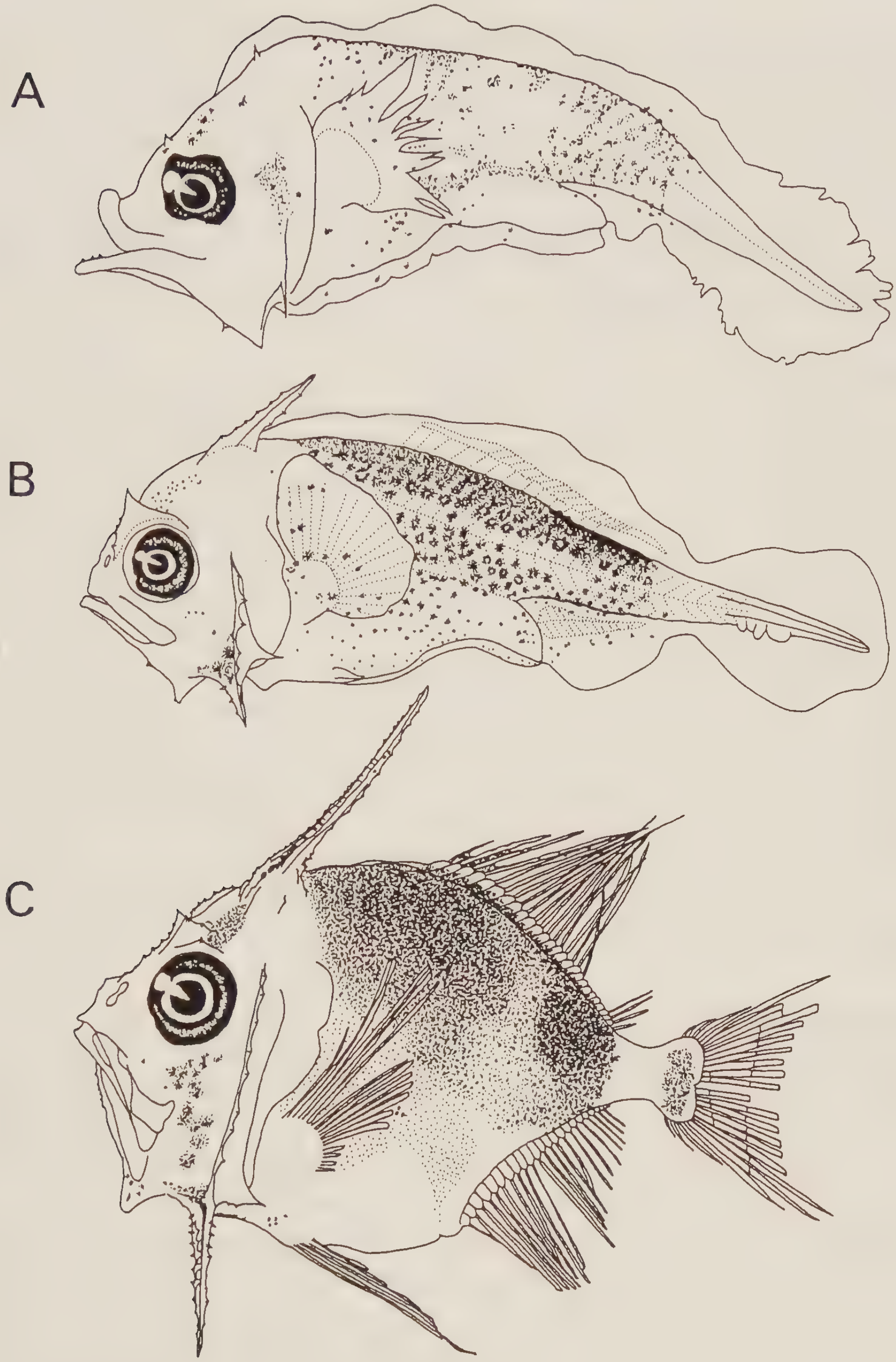


Fig. 7. Larvae of *Diretmichthys parini*. A) 3.2 mm NL; B) 6.0 mm NL; C) 8.8 mm SL.

fin base and the anal-fin origin, the preanal length (55% SL) relatively shorter than that of the preflexion larvae.

The 8.8 mm larva is lacking in scales and scutes. Larvae of *D. parini* of 13 to 14 mm SL first develop scutes on the midventral keel posterior to the pelvic-fin base (Post and Quero, 1981). For an examination of larval squamation, large specimens more than 8.8 mm SL are needed; they probably possess spiny scales only on the ventral midline of the anterior trunk, as in other diretmid larvae (Baldwin and Johnson, 1995).

Fins and Meristics

In the 3.2 mm larva, the pectoral fin is membranous, and the median finfolds extend along the body posterior to the eye. The pelvic fin is lacking. The 6.0 mm larva has a small, membranous pelvic fin under the pectoral-fin base, and the dorsal- and anal-fin anlagen located in the finfold. The larva of 8.8 mm SL has a full complement of rays in all fins: the dorsal fin (28), anal fin (21), pectoral fin (17), pelvic fin (7), and principal caudal fin (10+9). The large pectoral fin is posterodorsally oriented, the longest ray reaching to the dorsolateral area of the trunk. The pelvic fin is long, and its tip is beyond the anal-fin origin. A tiny spine, which originates from a distal radial of the dorsal and anal pterygiophores, is present laterally on the bases of first 23 dorsal-fin rays and about 12 middle rays of the anal fin. Otherwise, none of fin rays are ornamented by spiny elements. However, adult *D. parini* bears spination on the lateral surface of the dorsal- and anal-fin rays (Kotlyar, 1990).

Thirty-two vertebrae are countable in the 8.8 mm larva. There are eight branchiostegal rays without spination.

Pigmentation

In the two preflexion larvae of 3.2 mm and 6.0 mm NL, the trunk including the anterior half of the tail is densely pigmented, which is arranged along myomeres, and is sparse mid-laterally. Melanophores are scattered on the gut and pectoral fin. The ventral finfold is lightly pigmented. Pigment is present on the head around the eye. The larger preflexion larva of 6.0 mm NL also has pigment on the cheek, preopercular spine and medial base of the parietal spine. In the 8.8 mm postflexion larva, the trunk, excluding the abdomen, and the tail anterior to the caudal peduncle are entirely pigmented: the areas over the pectoral fin and between posterior rays of the dorsal and anal fins are heavily pigmented. A patch of pigment is present on the base of the caudal fin. Dorsal-fin membrane among the first four rays is dark. The prolonged spines of the parietal and preopercle

bear pigment on their basal portions. The isthmus is slightly pigmented. Melanophores disappear on the pectoral fin.

Head Spination

In the 3.2 mm larva, a needlelike spine appears on the preopercle, and a tiny spine is present on the otic region, lower jaw, and over the eye. These spines except that on the lower jaw become enlarged and complicated with serrations or serrate ridges in the 6.0 mm larva; the preopercle has an additional spine projecting backward. In the 8.8 mm larva, the parietal and preopercle spines are notably prolonged, their lengths 86% HL and 59% HL, respectively. Other head spination of the intact larva is greatly similar in appearance and configuration to that of the cleared and stained specimen of larval *D. pauciradiatus* in 7.6 mm SL described previously. Appendix Figures 2B and 2C show the scanning electromicrograph of the base of the parietal spine of a 6.4 mm larva.

Family ANOMALOPIDAE

The Family Anomalopidae (Flashlight fishes), consists of six genera, *Anomalops* (one species), *Kryptophanaron* (one species), *Photoblepharon* (two species), *Parmops* (one species), *Phthanophaneron* (one species) and *Protoblepharon* (one species), their adults being characterized by subocular luminous organs (Nelson, 1994; Baldwin *et al.*, 1997). In the tropical and temperate waters of the western North Pacific, two flashlight fishes, *A. katoptron* and *Photoblepharon palpebratus*, are distributed (McCosker and Rosenblatt, 1987). *Anomalops katoptron* is distinguished from *Photoblepharon* in having fewer soft rays of the anal fin (10–11 vs. 13–15) and two dorsal fins (McCosker and Rosenblatt, 1987; Colin, 1989).

Very little is known about early life stages of anomalopids; descriptions and illustrations of three yolk-sac larvae (3.3–3.8 mm NL), and one flexion (4.1 mm NL) and two postflexion larvae (5.8 mm SL) of *A. katoptron* were made by Colin (1989) and Konishi and Okiyama (1997), and those of 6.2 mm NL flexion larva of *K. alfredi* by Baldwin and Johnson (1995).

In this chapter, descriptions and illustrations of larval *A. katoptron* identified by anal-fin count and collecting locality are nearly completely reproduced from Konishi and Okiyama (1997).

Anomalops katoptron
Figure 8

General Morphology

Although the yolk-sac larvae of *A. katoptron* (Colin, 1989) and a flexion larva of *K. alfredi* (Baldwin and Johnson, 1995) are considerably elongate, a 5.8 mm SL postflexion larva of *A. katoptron* examined (Fig. 8A) is disk-like and quite laterally compressed (body depth 56% SL at pectoral-fin base). The head is large and its length occupies nearly one-half body length. The eye occupies 33% of head length and is round. The snout (25% HL) is blunt. The terminal mouth is oblique and large, its posterior margin extending slightly beyond the center of the eye. There are about ten tiny teeth along the anterior half of the premaxilla and several small teeth on the anterior portion of the dentary. The gut is coiled, and the anus is posteriorly situated just before origin of the anal fin (preanal length 63% SL).

A 4.1 mm NL flexion larva has a laterally curved, small, slightly pigmented projection on right side of the ascending process of the premaxilla. But, presence of this projection on opposite side is uncertain. In a 5.8 mm SL postflexion larva, superficially unpigmented, crescent-shaped tissues lie beneath each eye. These tissues may represent the incipient luminous organs.

Both larvae have scales with one to four spinules projecting nearly perpendicular to the scale plate (Appendix Figs. 3A, 3B). In the larger specimen, spinous scales cover the body except the caudal peduncle and the area around the pectoral fin. Twenty-seven scales are countable in a longitudinal series from the posttemporal to the caudal peduncle. About 15 small scutes are aligned on the abdominal keel from the base of the pelvic fin to near the anus.

Fins and Meristics

The fins of the 5.8 mm SL larva are well developed, although the rays are very feeble. The tips of the fins except the densely pigmented, elongate pelvic fin are slightly destroyed. The larva has a full complement of dorsal-fin rays (V-I, 14), anal-fin rays (II, 10), pelvic-fin rays (I, 5), and principal caudal-fin rays (10+9), but the pectoral fin is incomplete. Rays of the first dorsal fin of this specimen are longer than those of the second dorsal fin, especially the anteriormost two rays of the first dorsal fin which are prolonged and at least 85% HL, in contrast with a 6.2 mm NL larva of *K. alfredi* (Baldwin and Johnson, 1995) which has the shorter rays of the first dorsal fin. The pelvic fin is formed in the 4.1 mm flexion larva precociously, its origin being under the pectoral-fin base. In the

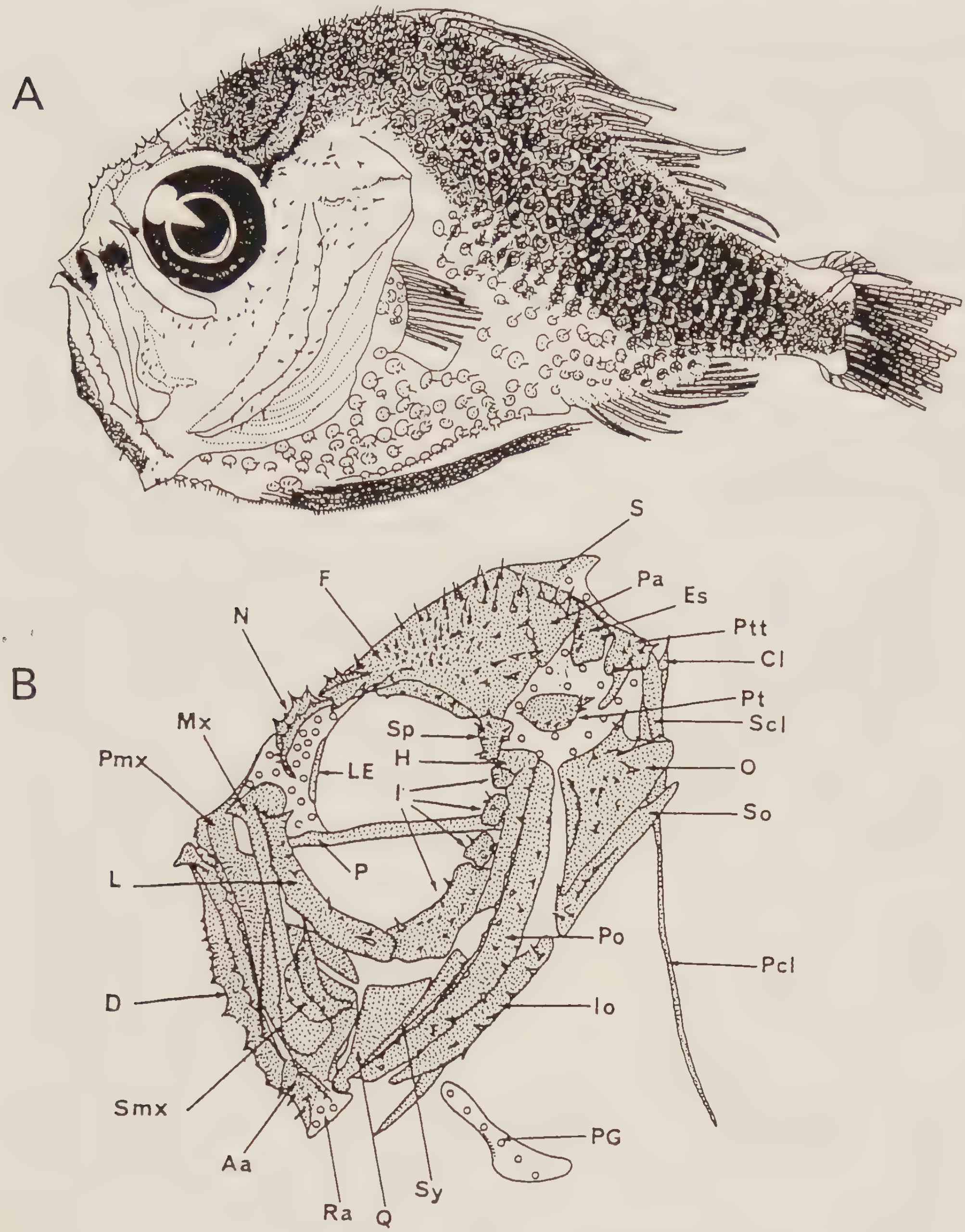


Fig. 8. Larva of *Anomalops katoptron* in 5.8 mm SL: A) whole appearance; B) head spination (after Konishi and Okiyama, 1997). Larger stippling in the figure represents cartilage. F–frontal, N–nasal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, S–supraoccipital, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Pcl–postcleithrum, Cl–cleithrum, PG–pelvic girdle.

larger specimen, the pelvic fin is inserted in the isthmus and quite prolonged, its tip reaching to the anal-fin origin. All fins except the pectoral fin bear spinules laterally on all rays (for the pelvic and caudal fins, Appendix Figs. 3C, 3D). Spinules also occur on the upper 4 and lower 3 procurrent spines of the caudal fin.

There are eight branchiostegal rays, none of which have spinules or serrations. But adult *Anomalops katoptron* (BSKU 8879) bears spination on the lower limbs of the anterior three branchiostegal rays, in addition to spination on all rays of all fins.

Pigmentation

Larval *Anomalops* has a peculiar pigment pattern. In the 5.8 mm SL larva, a wide pigment band extends uninterruptedly from the dorsal side of the head to the base of the caudal fin; pigment in this band is most dense in areas between scales, as seen in a larval *K. alfredi* (Baldwin and Johnson, 1995). The tip of the upper jaw and the ventral side of the entire lower jaw are heavily pigmented. The anal fin has a line of pigment at the base of the middle fin rays, but the dorsal fin is unpigmented. The elongate pelvic fin is dark, as in larval *Aulotrachichthys* (Fig. 11; Jordan and Bruce, 1993), *Kryptophanaron* (Baldwin and Johnson, 1995), and *Monocentris* (Fig. 9; Okiyama, 1988b). Small melanophores are scattered on the caudal fin. This pigment is not present in the other beryciform larvae excluding *K. alfredi* (Baldwin and Johnson, 1995), consequently being shared by only two anomalopid larvae. Pigment pattern of *A. katoptron* described above appears essentially the same in the 4.1 mm larva.

Head Spination

Head ornamentation of the larva of 5.8 mm SL (Fig. 8B) is present on many of the exposed bones, and is slightly more simple than those of larvae of three trachichthyids described below. On the frontal, an obliquely oriented, slightly serrate ridge is present at the anterior margin, and numerous, small spines occur on the remaining portion. The supraorbital ridge bears a few tiny spines. Each bone of the infraorbital series including the lachrymal has some spines on the lateral and distal regions. A longitudinally oriented, deeply serrate ridge occurs at both edges of the nasal. The parietal bears an obliquely oriented ridge with deep serrations. There are five small spines or so on each bone of the extrascapular, pterotic and sphenotic. Several tiny spines occur on the supramaxilla laterally. The dentary bears two parallel, serrate ridges ventrolaterally. The anguloarticular has a slightly serrate, low ridge, beneath which there are four spines. The boomerang-like preopercle bears a slightly serrate ridge along the entire length of the

anterior margin. More than ten spines are present on the lateral face of the preopercle. The opercle has a low ridge with three spines on the dorsoposterior portion. Some low ridges or spines are present on the lateral surface of the opercle, subopercle and interopercle. The medial posttemporal bears a serrate ridge and four spines. A single spine is present dorsoposteriorly on the supracleithrum.

Adult *Anomalops katoptron* (BSKU 8879) essentially retains the larval head and fin spination with changes in the configuration and size of spines; furthermore, it has an ornamented maxilla and spinules on pectoral-fin rays that are absent in the 5.8 mm SL larva.

Family MONOCENTRIDAE

The Family Monocentridae (Pinecone fishes) is characterized by large, heavy platelike scales and phosphorescent light organs on the lower jaw, and is distributed in the tropical and subtropical waters of the Indian and Pacific Oceans (Nelson, 1994). The family consists of two genera with four species: *Cleidopus gloriamaris* only from Australia, *Monocentris japonicus*, *M. neozelanicus* only from New Zealand, and *M. reedi* only from the southeastern Pacific (Kotlyar, 1985). Paxton *et al.* (1989) placed *M. neozelanicus* in the synonymy of *M. japonicus*. Kotlyar (1985) reported that the light organ of *Monocentris* is present on the symphysis of the lower jaw, whereas that of *Cleidopus* is located on the posterolateral surface of the lower jaw; *M. japonicus* differs from *M. reedi* in the numbers of gill rakers on the first gill arch (15–20 vs. 22–25) and lateral-line scales (12–17 vs. 17–20) (Kotlyar, 1985); only *M. japonicus* is distributed in the western North Pacific including Japan and its adjacent waters.

Information about larval monocentrids is restricted to *Monocentris* (Uchida, 1932; Yamada *et al.*, 1979; Okiyama, 1988b), but it is not sufficient to consider relationships within the Trachichthyoidei.

In this study, a description of larval *M. japonicus* is made by reference to Okiyama's (1988b) information. His drawings of four larvae of 3.4 mm, 5.8 mm, 6.5 mm and 13.0 mm SL were measured to obtain morphometric data, and the meristic characters such as fin rays and scales were counted. Additionally, 3 specimens of 5.7 mm, 5.8 mm and 8.5 mm SL were used to determine the details of body oranamentation.

Monocentris japonicus
Figures 9, 10

General Morphology

Although a reared preflexion larva of 3.4 mm NL has a moderately deep body, the body of specimens more than 5.8 mm SL is laterally compressed, and becomes deep (Fig. 9). The head is initially moderate in length, and becomes large with growth of the body. The eye is large and round. The terminal mouth is oblique and small in the 3.4 mm larva. Thereafter, the mouth grows large, the posterior tip nearly extending to beneath the posterior margin of the eye. In the 8.5 mm cleared and stained larva, there are two rows of teeth covering the entire length of the premaxilla, and five small teeth on the anterior area of the dentary. The gut is straight in the 3.4 mm larva, and becomes coiled later. The anus is situated posteriorly beyond the mid body.

The incipient, black-colored light organ appears on the symphysis of the lower jaw of the 6.5 mm larva. Unusual scales with a pyramid-shaped configuration are forming on the lateral surface of the trunk of the 5.8 mm larva. In the 6.5 mm larva, the scales are arranged sparsely in 6 longitudinal rows on the trunk, and 11 scales are countable on the lateral line, close to the adult complement of 12–17; several scales on the gut are larger than the others. An additional row of scales is present on the dorsal midline of the predorsal area and the dorsolateral surface of the body from the predorsal region to the posterior dorsal-fin base in the 8.5 mm larva. A detailed examination of scales of the 5.7 mm larva reveals that erect spinules occur in a row on each ridgeline of the pyramid-like scales (Appendix Fig. 4). Six scutes are aligned on the abdominal keel from the cleithral symphysis to the anus.

Fins and Meristics

The 3.4 mm larva has no fins except a small, membranous pectoral fin. Finfolds extend along the body posterior to the head. In the 5.8 mm larva, incipient rays are present in all fins. The 6.5 mm larva has a full complement of fin rays. Fin-ray counts of the 8.5 mm larva are as follows: dorsal-fin rays (VI, 12), anal-fin rays (10), pectoral-fin rays (15), pelvic-fin rays (I, 3) and principal caudal-fin rays (10+9). Contrary to the stout spines of the dorsal and pelvic fins of adults, larvae have very feeble spines of both fins. Spinous elements of the adult dorsal fin are not joined by membranes, and the spinous dorsal fin is separate from the soft dorsal fin. But, the 6.5 mm and 8.5 mm larvae have a single dorsal fin with spines and soft rays.

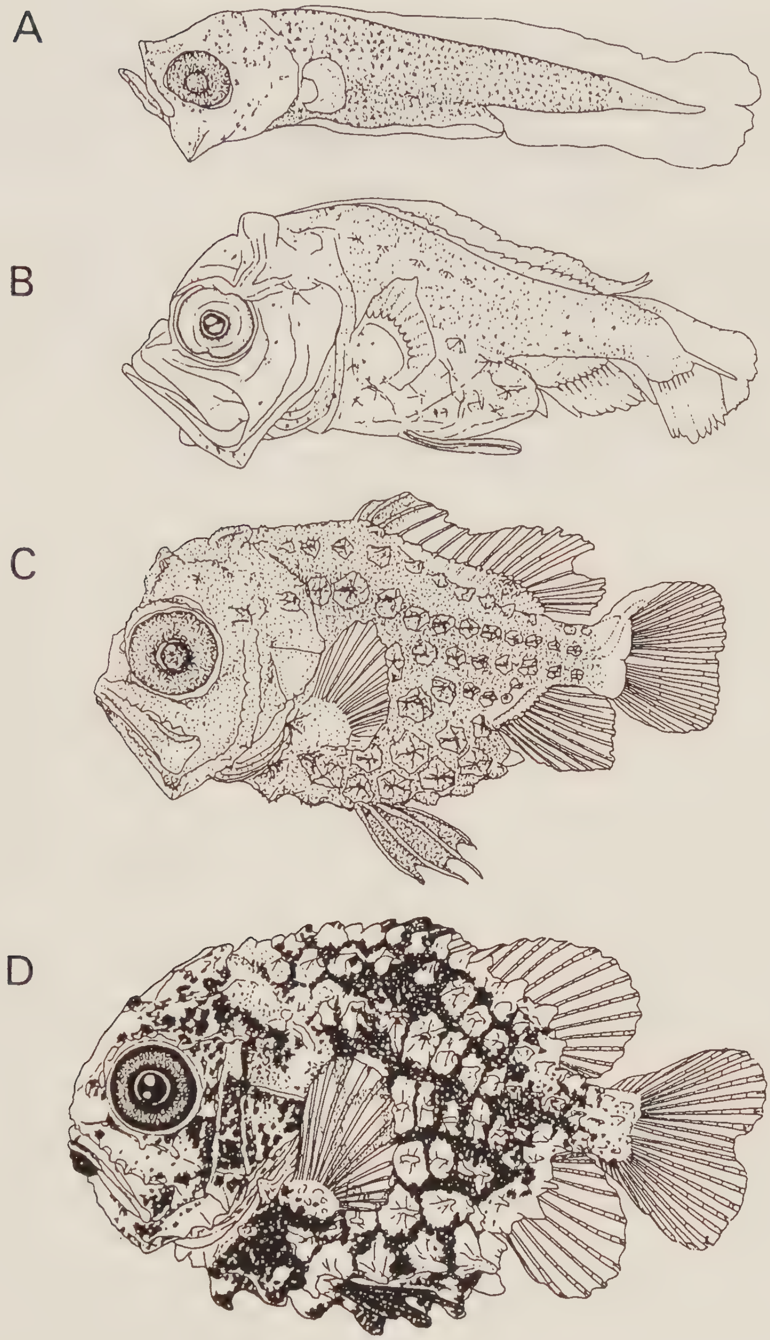


Fig. 9. Larvae of *Monocentris japonicus*: A) 3.4 mm NL; B) 5.8 mm SL; C) 6.5 mm SL; D) 13.0 mm SL (after Okiyama, 1988b).

The 8.5 mm larva has the adult complement of 26 vertebrae and 8 branchiostegal rays. The specimen has no spination on fin and branchiostegal rays, but an adult *M. japonicus* (BSKU 8844) has oranamentation with tiny spines on some branchiostegal rays and all fin rays except three soft rays of the pelvic fin.

Pigmentation

Pigment is well developed in the early life stages from hatching to juvenile. In a yolk-sac larva just after hatching, the body except the tip of the tail is dark (Yamada *et al.*, 1979). The same pigment pattern is present in the 3.4 mm larva, but pigment on the head becomes somewhat sparse. Additional pigment occurs on the dorsal fin between the first three rays, the posterior region of the dorsal-fin base and the pelvic fin in the 6.5 mm larva.

Head Spination

The head of the 3.4 mm larva is not adorned with spiny elements. The spination begins to form in larvae by 5.8 mm SL. Head spination of the 8.5 mm larva is unusual in configuration, particularly on the skull roof (Fig. 10). The frontal has a slightly high, outward projecting, spiny ridge on the dorsolateral surface, a low, serrate ridge on the lateral surface, and a small ridge with two spines on the anteriormost area. The dorsolateral ridge actually consists of three relatively long, branched, serrate ridges, which are joined to each other. Each of the three ridges additionally bears short, serrate or non-serrate ridges on the lateral surface. The joint of the three ridges forms a summit, and possesses a patch of tiny spines. A supraorbital ridge projecting outward has short, serrate ridges on the dorsal surface, and spines on the outer margin. The lachrymal and first two infraorbitals bear a spiny ridge on their upper margins, and spines on the lower margins. A small number of spines lies on the anterior and posterior margins of the last two infraorbitals. The sphenotic has several spines. The nasal bears a serrate ridge on the lateral and medial margins. A remarkably outward projecting, bony plate on the parietal possesses serrate ridges and a patch of small spines on the dorsal and ventral surfaces, and serrations on its anterior and posterior margins. Two small spines are present on the extrascapular. The pterotic has a wen-like projection with a patch of small spines and serrate ridges on the middle region, and several spines on the posterior margin. No ornamentation appears on the supraoccipital, over which only a spinous scale is present. The supramaxilla has a serrate ridge on the lateral surface, and spines on the lower margin. A serrate ridge and a spine occur on the dentary. The posteroventral corner of the anguloarticular has a group of small spines. The preopercle bears a

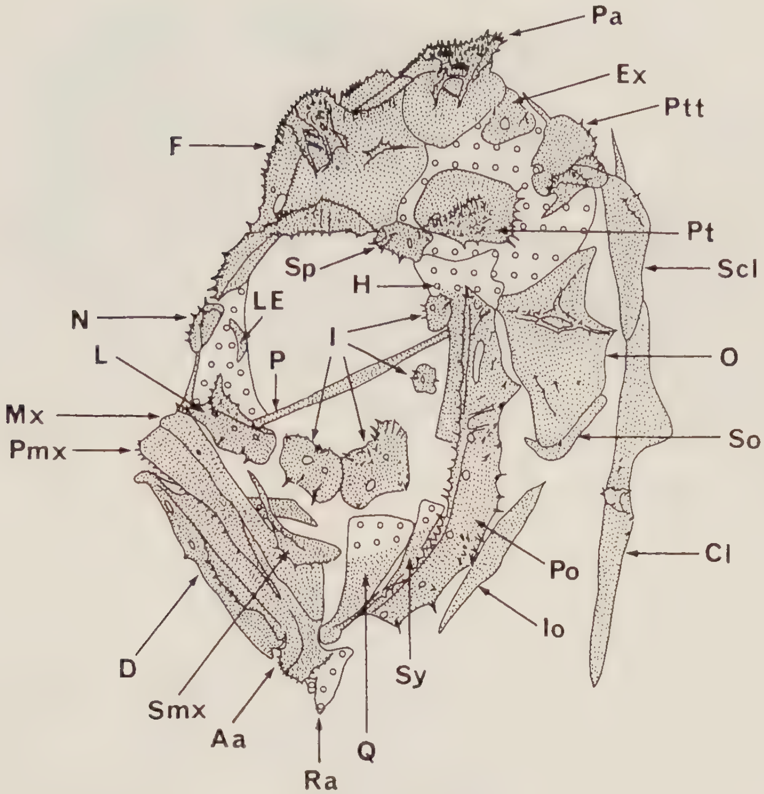


Fig. 10. Head spination of *Monocentris japonicus* in 8.5 mm SL. Larger stippling in the figure represents cartilage. F–frontal, N–nasal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Cl–cleithrum.

long, serrate ridge on the entire length of the anterior margin, and some spines on the lateral surface and posterior margin. On the opercle, there is a three-branched ridge with spines on the dorsolateral surface, and two obliquely oriented, serrate ridges and a spine on the ventrolateral area. The subopercle has a tiny spine. The rod-shaped interopercle develops no spination, but Baldwin and Johnson's (1995) specimens have it. The posttemporal possesses a trough-shaped, spiny ridge on the lateral surface, and spines on the posterior margin. The supracleithrum has a short, serrate ridge and a spine on the dorsolateral region. A spiny protuberence and several small spines occur on the lateral surface of the cleithrum. The presence of this spination is unique in trachichtyoid larvae.

Family TRACHICHTHYIDAE

The Family Trachichthyidae (Roughies) consists of seven genera, *Aulotrachichthys, Gephyroberyx, Hoplostethus, Optivus, Paratrachichthys, Sorosichthys*, and *Trachichthys*, with about 33 species, about half of which are placed in *Hoplostethus* (Nelson, 1994). The number of the dorsal–fin spines, position of the anus, rotundity of the body and combinations of those features are distinguishing adult characters of each genus within the Trachichthyidae (Woods and Sonoda, 1973). Three genera, *Aulotrachichthys, Gephyroberyx* and *Hoplostethus*, with six species occur in Japan (Hayashi, 1993b ; Yamada *et al.*, 1994).

In this chapter, descriptions and illustrations of larvae of three trachichthyids are nearly completely reproduced from Konishi and Okiyama (1997).

Aulotrachichthys sp.
Figure 11

Aulotrachichthys, originally established as a subgenus of *Paratrachichthys* by Fowler (1938), is distinguished from *Paratrachichthys* by having striated tissues on the ventrolateral portion of the body (Fowler, 1938). Paxton *et al.* (1989) considered *Aulotrachichthys* an independent genus based on the above character. Morphological differences in head and dermal spination, size at caudal flexion, and size and pigmentation of the pelvic fins between larvae of *Aulotrachichthys* and *Paratrachichthys* in the Australian waters (Jordan and Bruce, 1993) corroborate the existence of these two genera. Jordan and Bruce (1993) described larvae of Australian *Aulotrachichthys* sp. with a series of whole specimens (not cleared and stained), but their descriptions of body ornamentation are not complete.

In this section, larval morphology of Japanese *Aulotrachichthys* sp. (*A. prosthemius* or *A. sajademalensis*, which have nearly same fin–ray counts) from 4.6 mm NL to 10.9 mm SL is reproduced from Konishi and Okiyama (1997).

General Morphology

The body is laterally compressed and extremely deep (body depth at the pectoral–fin base 41% NL to 65% SL). The head is also large, occupying 35% to 56% SL. The eye is large and its diameter is about one third of head length. The terminal mouth is oblique and large, the posterior margin of the upper jaw extending beyond the eye. About 20 tiny teeth are present on the premaxilla in the 7.4 mm larva (Fig. 11A). In the 4.6 mm larva, the anus is situated in the

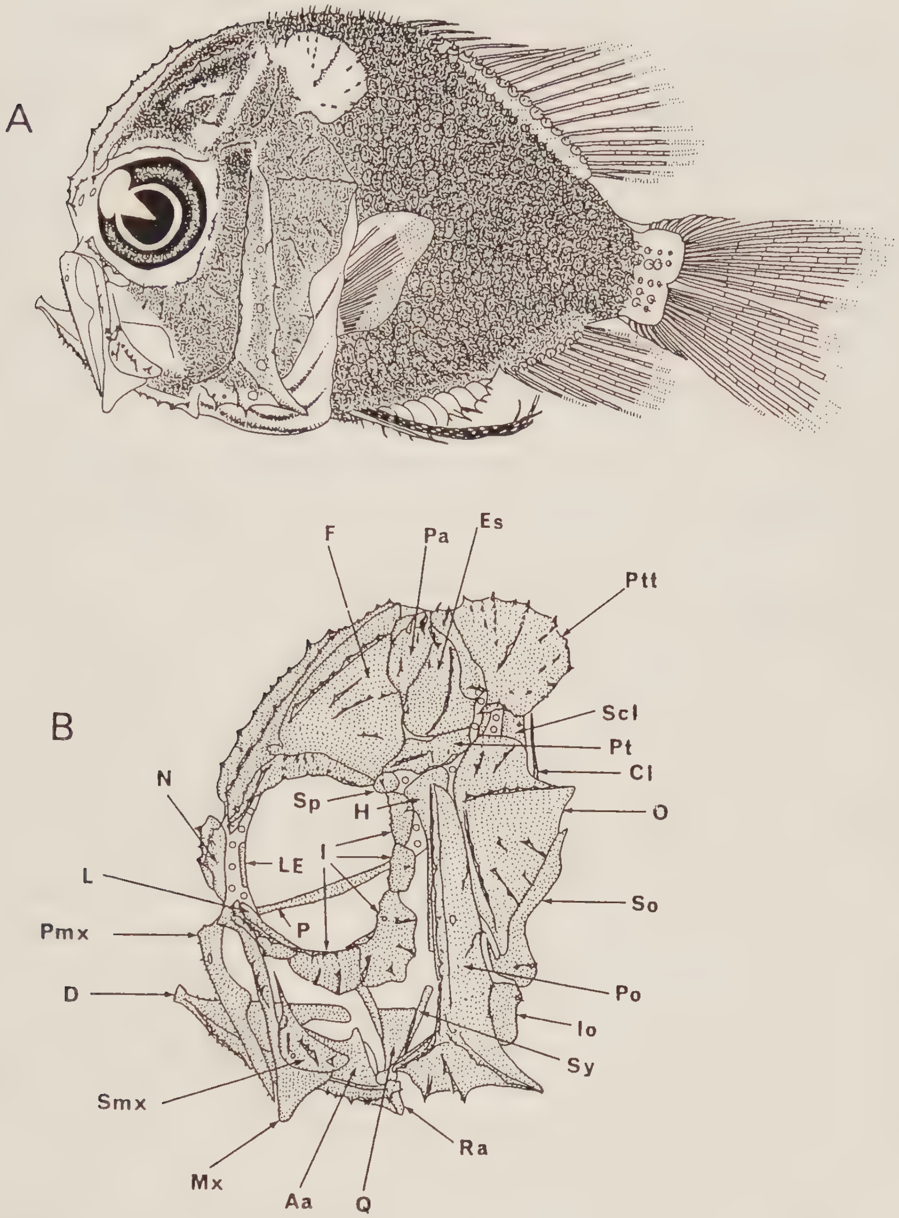


Fig. 11. Larva of *Aulotrachichthys* sp. in 7.4 mm SL: A) whole appearance; B) head spination (after Konishi and Okiyama, 1997). Larger stippling in the figure represents cartilage. F–frontal, N–nasal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Cl–cleithrum.

adult position between the bases of the pelvic fins and is surrounded by black, doughnut-like glandular tissue.

The 4.6 mm larva is not scaled. In the 7.4 mm postflexion larva, distinctive scales are well developed on the body except the head, axillary portion of the pectoral fin and striated tissues extending from pelvic- to anal-fin base. The longitudinal scale count is 27. Each scale has one to two (usually 2) slightly erected spinules. Spinules may be added with growth of body; 2–3 spinules occur on scales in a 19.0 mm SL postflexion larva of *Paratrachichthys prosthemius* (= *Aulotrachichthys prosthemius*) collected from Hawaii (Gon, 1987). Eight scutes are present on the abdominal keel between the pelvic-fin base and the anal-fin origin in the 7.4 mm larva.

Striated tissue is developed in the ventrolateral portion from the pelvic-fin base just beyond the posterior end of anal-fin base, and on the isthmus inside of gill cavity in the 7.4 mm larva.

Fins and Meristics

In the 4.6 mm NL larva, all fins are developing, and the densely pigmented pelvic fin is prolonged and has a full complement (7) of fin elements. The 7.4 mm SL larva has an adult complement of rays in the dorsal fin (V, 13), anal fin (Ⅲ, 8), pectoral fin (13), pelvic fin (Ⅰ, 6), and principal caudal fin (10+9). Larvae between 7.4 mm and 9.7 mm SL possess 2 or 3 spinules on the sixth soft ray of the pelvic fin, although spinules are absent on fin elements of the 4.6 mm SL larva. In the 10.9 mm SL larva, most rays of all fins bear spinules laterally. Two other larvae, 4.5 mm and 5.9 mm SL, which were collected on 25–26 June in 1991 about 150 miles west of Saipan in the Marianas, and may be another type of *Aulotrachichthys*, have spinules on the rays of all fins.

There are eight branchiostegal rays in the 7.4 mm SL specimen, and a single spinule appears ventrally on the fourth ray. Each of the middle six branchiostegal rays of the 10.9 mm larva bears several spinules.

Pigmentation

Pigmentation of larvae is well developed. In the 4.6 mm NL specimen, melanophores uniformly cover nearly the whole body except for the posteriormost part of body, dorsal, anal, pectoral, and caudal fins and their bases. The pelvic fin is heavily pigmented. Pigment also occurs on the lateral surface of the upper jaw, the ventral side of the lower jaw and the branchiostegal rays. The 10.9 mm SL larva essentially retains the above pigment pattern, additionally having the pigmented dorsal- and anal-fin bases.

Head Spination

Head bones of the 7.4 mm SL cleared and stained larva are well ornamented and ossified (Fig. 11B). The frontal bears two longitudinal, serrate ridges: from a dorsal view, a short, slightly arched ridge, approximately parallel with the dorsal midline, is associated anteriorly with the inner ridge of the nasal; and a long ridge that forms an angle of about 30 degrees with the midline at its posterior portion extends to the anterior tip of the supraorbital. Each frontal also has four obliquely oriented, relatively low, serrate ridges on the lateral surface. Several rows of minute spines are present on the supraorbital ridge. Each infraorbital bone has a laterally extending, low, serrate ridge or three minute spines on the inner margin, and a serrate ridge or spine on the lateral surface. The trough-shaped nasal bears a single serrate ridge on the lateral and medial margins. In the otic region, the parietal bears a ridge with three spines on its upper edge, two spines near the base of that ridge, and one spine and a vertically oriented ridge with two spinules on the lateral surface. The extrascapular largely covers the posterior portion of the parietal, and has a long, vertically arched, serrate ridge and a short ridge with two spines on the lateral surface. This bone also bears two short, serrate ridges on the dorsolateral region. A short, serrate ridge and one spine are present on the lateral surface of the pterotic. The maxilla and supramaxilla are ornamented; 3 spines on the mid-maxilla, 4 short, obliquely oriented, serrate ridges on the supramaxilla. Two serrate and parallel ridges are present on the ventrolateral margin of the dentary. The anguloarticular bears a horizontally oriented, serrate ridge on its lateral surface. A long and serrate ridge is present along the anterior margin of the preopercle. A large triangular-shaped spine occurs at the angle of the posterior margin of the preopercle, its lateral surface bearing an obliquely oriented, serrate ridge, which joins anteriorly the ridge on the anterior margin of the preopercle. On the lateral surface of the lower limb of the preopercle, a short, obliquely or vertically oriented, serrate ridge extends dorsally from the tip of each of two marginal, widely-spaced spines. There are three series of spinules or serrate ridges on the lateral surface of the upper preopercular limb. On the opercle, a horizontally oriented, relatively long, serrate ridge is present that anteriorly meets a vertically extended, serrate ridge. The opercle also bears two and four short, obliquely oriented, serrate ridges on its dorso- and ventrolateral surfaces, respectively. A short serrate ridge or one spinule occurs on the subopercle and interopercle. In the pectoral girdle, only the posttemporal is ornamented. The semicircular posttemporal laterally bears several radiately arranged rows of serrate ridges or spines.

As in the adults of *Hoplostethus* and *Gephyrberyx*, an adult *A. prosthemius*

(BSKU 38327) has well-developed head spination.

Hoplostethus sp.
Figures 12, 13

Hoplostethus comprises 23 species (Kotlyar, 1986b), of which three species, *H. japonicus*, *H. crassispinus* and *H. melanopus*, are distributed in Japan. Species identification of larvae of those species is difficult because they have overlapping meristic characters, such as fin-ray counts, number of lateral-line scales and vertebrae (Hayashi, 1993b; Yamada *et al.*, 1994).

Morphological information of larval or juvenile *Hoplostethus* is limited; Parr (1933, as *Korsogaster nanus*), Johnson (1970, as *K. nanus*), Konishi (1988b), and Konishi and Okiyama (1997). Very recently, Zeldis and Grimes (1998) reported development of eggs and yolk-sac larvae of *H. atlanticus*.

In this section, larval morphology of *Hoplostethus* sp. (presumably *H. japonicus* or *H. crassispinus* by fin-ray counts) based on three specimens, 5.4 mm NL, 9.6 mm SL and 10.7 mm SL, is reproduced from Konishi and Okiyama (1997).

General Morphology

The three larvae of *Hoplostethus* sp. are oval in shape and deep (body depth from 37% to 46% SL at the pectoral-fin base: Fig. 12). The head is moderately large and its length occupies one third of the body, usually becoming larger with growth. The proportions of body depth and head length to standard length are small in comparison with those of other trachichthyid larvae of nearly equivalent size. The eye is round and occupies 40 to 30% of head length. The snout (20% to 32% HL) is blunt. The mouth is oblique and large. Minute teeth on the premaxilla and dentary are developed in the larger two specimens. The anus is situated in the posterior portion of the body, and preanal length ranges from 63% to 77% SL.

In the 9.6 mm postflexion larva, scales are present from the predorsal region to below the mid point of the dorsal-fin base, in the lateral-line region, and ventrolaterally on the abdomen and isthmus. Unpored lateral-line scales with elliptical shape are extremely large in size and 23 in number. Each lateral-line scale regularly bears two nearly erect spinules (Appendix Figs. 5A, 5B). Scales in other areas are very small and round, and have only a single spinule. No scutes appear on the abdominal keel, but adults of *H. japonicus* (BSKU 39856), *H. crassispinus* (Hayashi, 1993b) and *H. melanopus* (Yamada *et al.*, 1994) possess them.

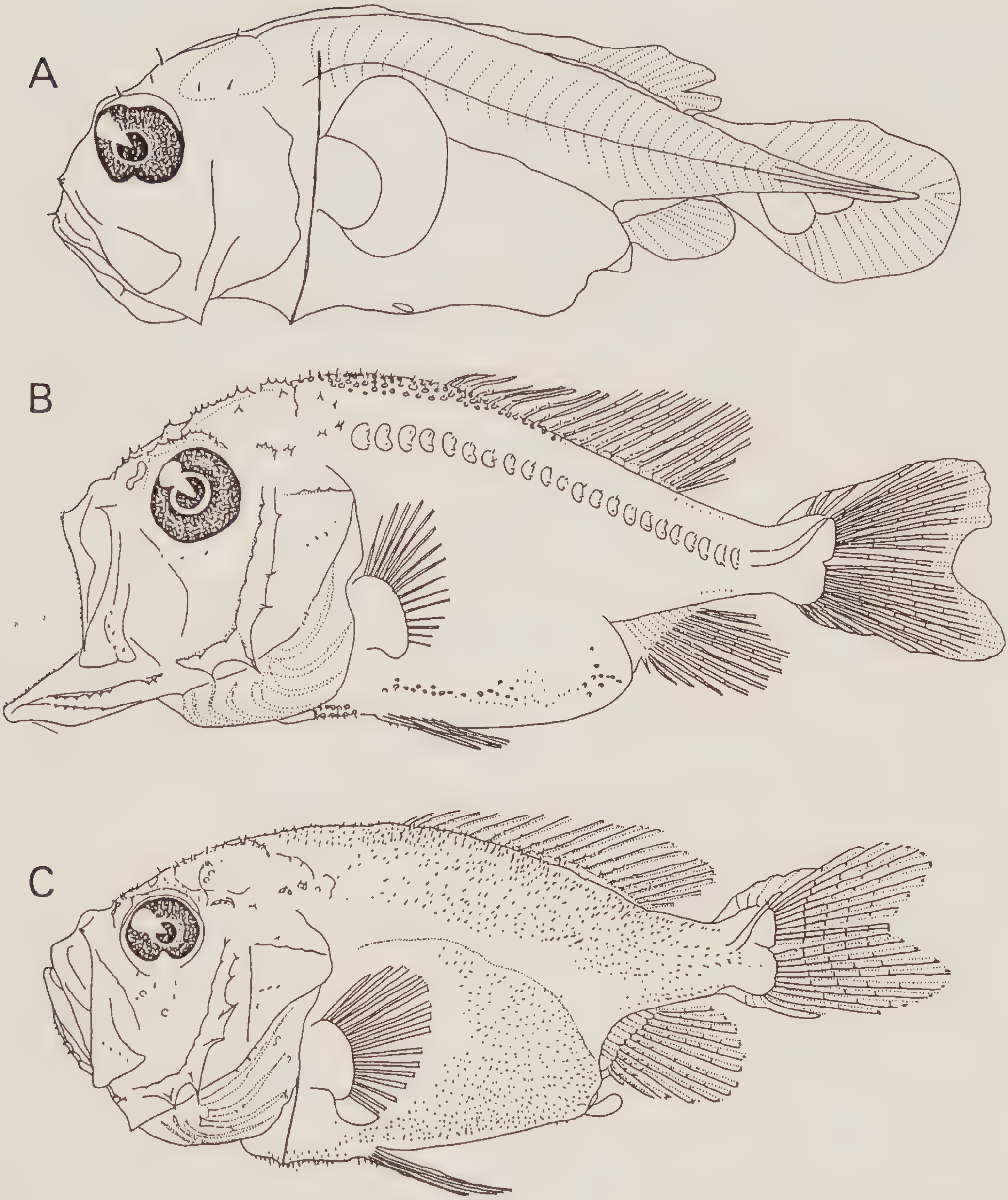


Fig. 12. Larvae of *Hoplostethus* sp.: A) 5.4 mm NL; B) 9.6 mm SL; C) 10.7 mm SL (after Konishi and Okiyama, 1997).

Fins and Meristics

In the 5.4 mm preflexion larva, the unpaired and pectoral fins are membranous, although the incipient rays are visible. The pelvic fin appears as a small bud posteriorly below the pectoral–fin base, not being precocious in comparison

with the larvae of *Anomalops katoptron* and *Aulotrachichthys* sp. of nearly equivalent size. Larvae of 9.6 mm and 10.7 mm SL have a full complement of rays in the dorsal fin (VI, 13), anal fin (III, 9–10), pelvic fin (I , 6) and principal caudal fin (10+9), but all fin spines are very weak and flexible. An adult complement of rays in the pectoral fin (17) has been achieved in 10.7 mm SL larva. This larva has spinules on the dorsal–, anal– and pelvic–fin rays (for dorsal–fin rays, Appendix Figs. 5C, 5D). Development of fin–ray spinules is more advanced in adult *H. japonicus* (BSKU 39856) and *H. melanopus* (Yamada *et al.*, 1994), although its occurrence on the caudal–fin rays is variable among species; absent in the former species, present in the latter. This variance may be present in larval stages, because Baldwin and Johnson's (1995) specimens of *Hoplostethus* sp. and *H. mediterraneus* have spinules on the caudal rays. A full complement of branchiostegal rays (8) is present in the 9.6 mm and 10.7 mm SL larvae, the latter of which has spinules on the 6th and 7th branchiostegal rays.

Pigmentation

There is no pigmentation on the three specimens examined; pigment may have been lost during the long preservation of 16 to 17 years. Juvenile *Korsogaster nanus* (=*Hoplostethus* sp. by Baldwin and Johnson, 1995) has numerous fine melanophores scattered on the body, a black peritoneum and densely pigmented membranes on the pectoral and pelvic fins (Johnson, 1970).

Head Spination

Larvae have a moderately ornamented head. In the 5.4 mm preflexion larva, three small spines are borne on the frontal, two on the otic region, and one on the parietal and dentary.

In the 9.6 mm cleared and stained specimen (Fig. 13), there are two longitudinal ridges with spines on the frontal. The anterior one with three spines is over the forebrain, and almost joins the inner ridge on the nasal anteriorly. The posterior ridge has a long base and about ten spines, and it lies over the midbrain. Under this ridge, there is a single frontal spine. The supraorbital has an obliquely oriented ridge with four spines, and several other scattered spines. Only two small spines are present laterally on the posterior portion of the long, stick–shaped lachrymal, and two small spines are on the first infraorbital. The trough–shaped nasal bears two short and parallel ridges with four and three spines on the inner and outer ridges respectively. Bones in the otic region exhibit well–developed bony projections. The parietal bears two spinous ridges: one is slightly curved, relatively high and longer with seven spines, the other has a single spine and

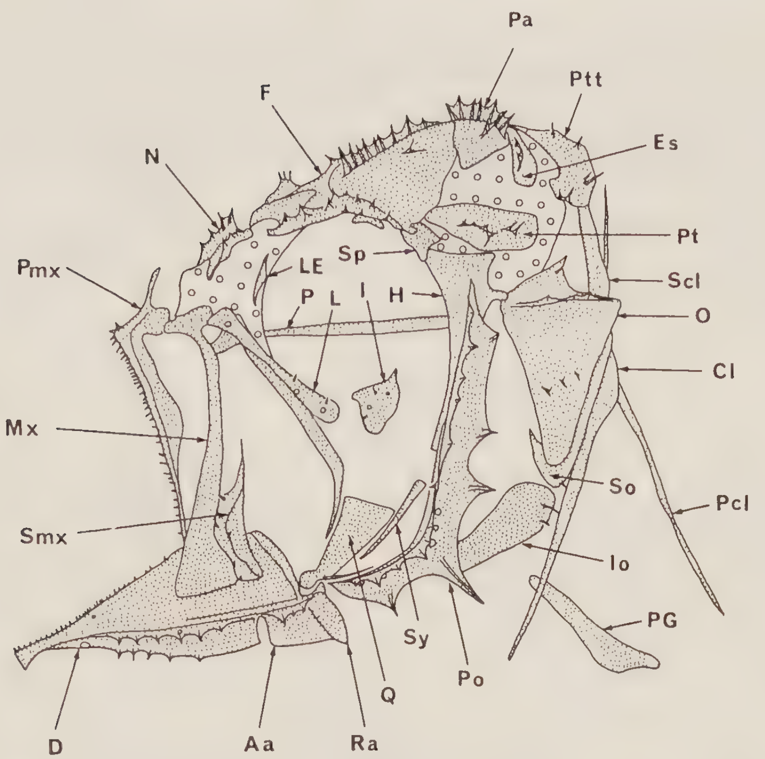


Fig. 13. Head spination of *Hoplostethus* sp. in 10.7 mm SL (after Konishi and Okiyama, 1997). Larger stippling in the figure represents cartilage. F–frontal, N–nasal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Pcl–postcleithrum, Cl–cleithrum, PG–pelvic girdle.

meets at nearly a right angle with the long ridge. A vertically curved, short ridge with two spines is present on the lateral surface of the extrascapular. There are two short ridges on the pterotic, the anterior one with four spines, the posterior with two spines. The supramaxilla has four spinules at the lower margin and one on the lateral surface. Two rows of nearly equally spaced spines are present on the dentary. The anguloarticular possesses a single ridge with three spines. The opercular series has well-developed spines and spinous ridges. At the posterior edge of the preopercle, five widely spaced spines occur; three on the upper limb, one on the lower limb, and the longest at the angle. A ridge with nine spines extends along nearly the entire length of the anterior margin of the preopercle. The opercle bears a low and straight ridge with three small spines longitudinally.

There are also three spinules obliquely arranged on the lateral surface of the opercle. Two needle-like spines are present on the posterior margin of the interopercle near its junction with the subopercle, which also has a single short spine. In the shoulder girdle, only the posttemporal has spinous elements, bearing six spines.

An adult *H. japonicus* (BSKU 39856) additionally has a spinous maxilla, and develops more advanced ornamentation on the opercular and infraorbital series, both jaws, the parietal and posttemporal.

Gephyroberyx japonicus
Figures 14, 15

Gephyroberyx comprises three species, *G. japonicus* in Japan, *G. philippinus* in the Philippines, and *G. darwini* from the Atlantic through the Indian Ocean to the south coast of Australia; *G. japonicus* and *G. philippinus* may be a single species (Woods and Sonoda, 1973). Very little is known about larval morphology of *Gephyroberyx* (Konishi, 1988a; Konishi and Okiyama, 1997).

In this sectioon, morphological development of larval *G. japonicus* is reproduced from Konishi and Okiyama (1997). A supplementary specimen of *Gephyroberyx* sp. in 3.4 mm NL (AMS I.32786-006) is also used to determine the formation of the dorsal and anal fins.

General Morphology

Bodies of larvae from 4.5 mm NL to 11.0 mm SL are deep and laterally compressed (body depth at the base of pectoral fin 49.2% to 58.7% SL; Fig. 14). The head is large and robust, occupying about 40% NL to 50% SL. The eye is moderately large and about one third of the head length. The mouth is oblique and large, the posterior margin of the upper jaw reaching nearly to a point below the posterior edge of the eye. In the 4.6 mm SL specimen, there are ten widely-spaced teeth on the premaxilla covering nearly its entire length, and several teeth are present on the anterior portion of the dentary. In the 11.0 mm SL larva, two or three rows of teeth are present on the anterior portion of the premaxilla, and teeth in both jaws increase in number and size. The anus is located in the posterior half of the body just anterior to the anal fin.

No scales cover any portion of the body in the 4.5 mm NL and 4.6 mm SL specimens. In the 11.0 mm larva, the cheek, trunk and tail are well scaled. Scales on the lateral line are larger in size than other scales, slightly constricted at the posterior edge and 28 in number; the first eighteen scales have a single pore on

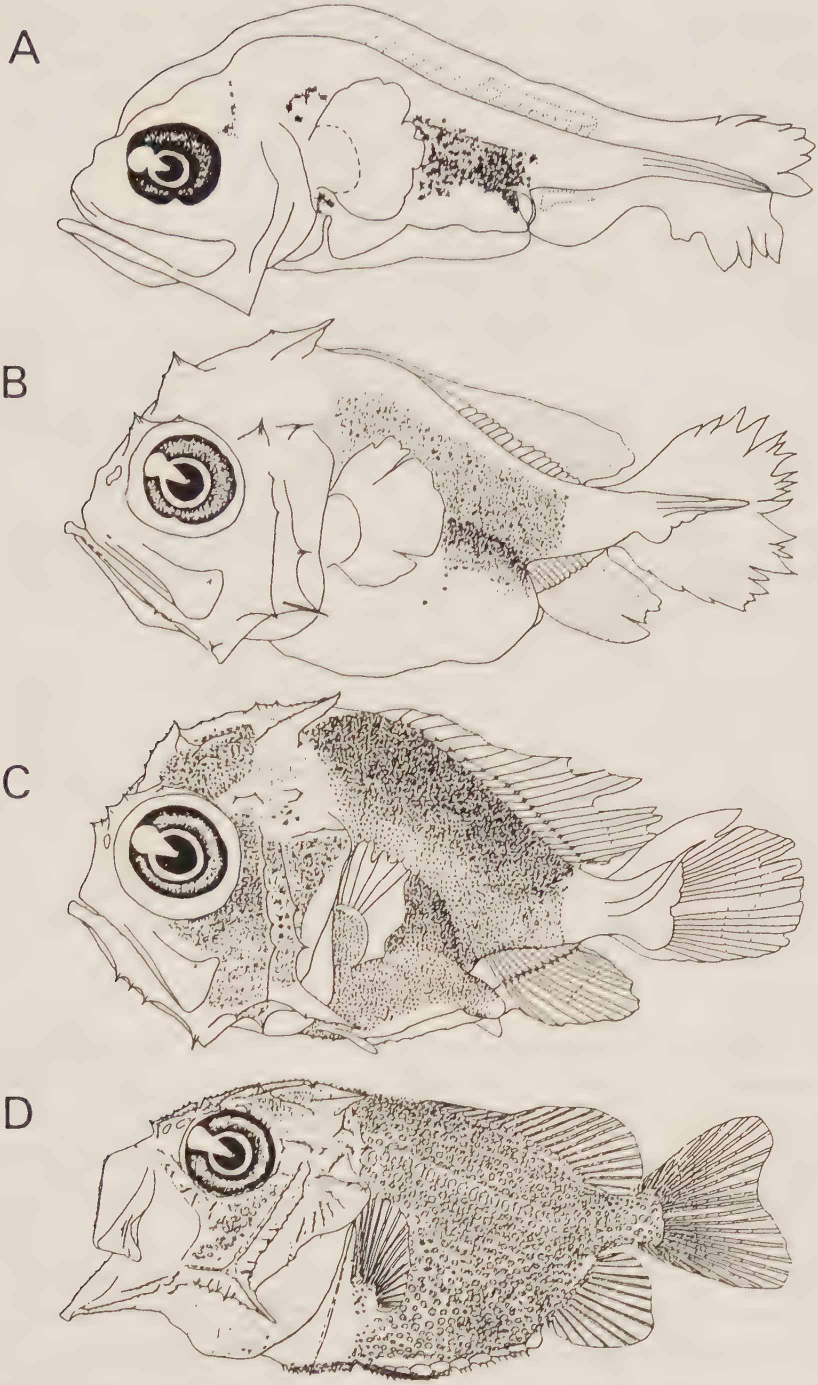


Fig. 14. Larvae of *Gephyroberyx* sp. (A–AMS I.32786–006, 3.4 mm NL) and *G. japonicus* (B–4.5 mm NL, C–4.6 mm SL, D–11.0 mm SL: after Konishi and Okiyama, 1997).

the anterior portion. Scales on the lateral line possess four erect spinules, whereas other scales have two or three erect spinules (usually, 2). Nine scutes occur on the abdominal keel from the base of the pelvic fin to the anus in the 11.0 mm specimen. Each scute bears a longitudinal ridge with three hook-like spines and two or three additional spines on the lateral surface.

Fins and Meristics

In the 3.4 mm NL preflexion larva of *Gephyroberyx* sp., the pectoral fin is membranous, and the median finfolds extend along the body. The anlagen of the dorsal and anal fins are situated in the finfolds. In the 4.5 mm NL larva of *G. japonicus*, fin development is proceeding in the unpaired and pectoral fins, but the pelvic fin is not present. Thus, this fin is not early forming, as observed in larval *Hoplostethus* sp.. The 11.0 mm SL larva has an adult complement of dorsal-fin rays (VIII, 13), anal-fin rays (III, 11), pectoral-fin rays (17), pelvic-fin rays (I, 6) and principal caudal-fin rays (10+9). All fins and the procurrent spines of the caudal fin in the 11.0 mm larva bear spinules basally.

There are eight branchiostegal rays, of which the fourth and fifth rays possess three and one spinule at their lower margins, respectively.

Pigmentation

Pigmentation of larvae is well developed. In the 4.5 mm NL larva, the dorso-lateral to peritoneal region of the trunk and the anterior portion of the lower jaw are pigmented. Pigment densely covers the entire body except for the caudal peduncle, snout, both jaws and fins in the 4.6 mm and 11.0 mm SL specimens.

Head Spination

Ornamentation of the head and shoulder girdle of larvae is well developed and very characteristic. In the 4.5 mm larva, spination appears on the frontal, otic region, supramaxilla, lower jaw and preopercle. In the 4.6 mm larva, head spines are larger, and additional spinous elements are present on the nasal and opercle. In both the 4.5 mm and 4.6 mm larvae, the parietal, frontal and preopercle spines are extremely prominent.

Figure 15 shows ornamentation of the head and shoulder girdle of the 11.0 mm SL cleared and stained larva. In the orbital region, the frontal has several longitudinal, curved or obliquely oriented ridges with serrations. Over the forebrain to the anterior portion of the midbrain, there is an outwardly arched ridge with thirteen spines. Perpendicular to the summit of this ridge is a short, concave, slightly serrate ridge. This ridge extends to and joins with a long, curved, serrate

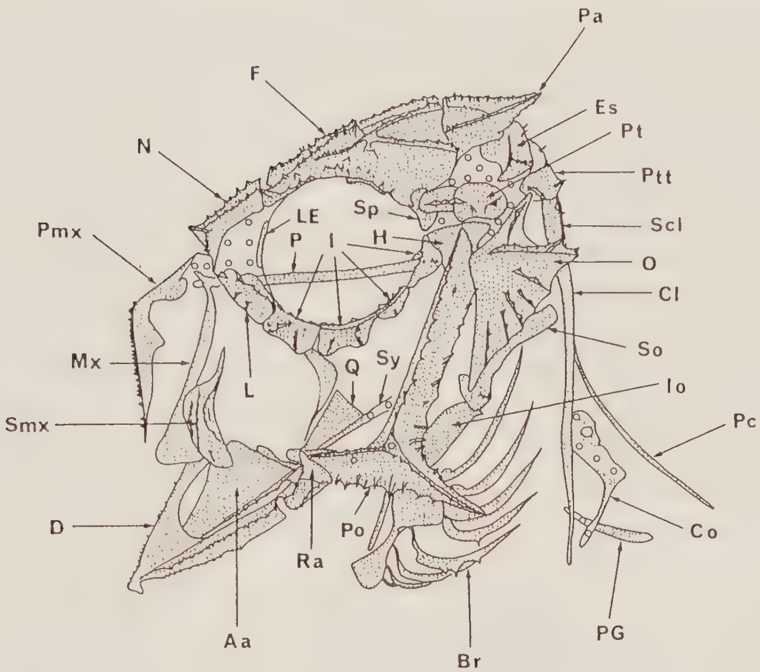


Fig. 15. Head spination of *Gephyroberyx japonicus* in 11.0 mm SL (after Konishi and Okiyama, 1997). Larger stippling in the figure represents cartilage. F–frontal, N–nasal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Br–branchiostegal ray, Ptt–posttemporal, Scl–supracleithrum, Pcl–postcleithrum, Cl–cleithrum, Co–coracoid, PG–pelvic girdle.

ridge that lies between the anterior margin of supraorbital ridge and the posterior margin of the frontal. On the orbital margin of the frontal, there are about twenty spines facing outward, and short ridges arranged like a web. The suborbital bones bear a series of low, arched, serrate ridges surrounding the lower portion of the eye, and nine low and radiated ridges with one to two tiny spines on the lateral surface. The inner and outer edges of the nasal bear a ridge with nine and eleven spines respectively. In the otic region, a unique spine triradiate in cross section and with finely serrate ridges is present on the parietal. The extrascapular has a vertically arched, low, serrate ridge, an obliquely straight, short, low, serrate ridge joined with the previous ridge on the lateral surface, and two small spines on the upper margin. The pterotic bears a low, short, serrate ridge and two spines on its lateral surface. One curved and two straight ridges with serrations, and two small

spines occur on the lateral surface of the supramaxilla. There are two rows of serrated ridges on the ventral side of the dentary, the outer ridge being more spinous. The anguloarticular has a relatively long, serrate ridge nearly parallel with dentary ridges, and two short, horizontal, serrate ridges on its lateral surface. The preopercle is characterized by a large spine at its angle. The anterior margin of the preopercle bears a curved, spine-bearing ridge along its entire length, and from its angle, a serrate, low ridge extends to the tip of the large spine. The posterior and lower edges of the preopercle also bear some sharp spines. The opercle has obliquely and horizontally oriented ridges with serrations on the lateral surface. A much shorter, low ridge with two small spines is present laterally on the lower portion of the subopercle. A spine occurs on the posterior margin of the interopercle near its junction with the subopercle. The posttemporal bears three small spines on the posterior margin, and a short, obliquely oriented, serrate ridge on the lower surface laterally. A small spine is present on the posterior edge of the supracleithrum.

An adult *G. japonicus* (BSKU 7237) possesses an ornamented maxilla, and develops more complex spination on the opercular and infraorbital series, both jaws, the parietal and posttemporal, as in adult *Hoplostethus japonicus* (BSKU 39856).

Family POLYMIXIIDAE

The Family Polymixiidae (Beardfishes), is characterized by having a pair of hyoid barbels, and consists of a single genus, *Polymixia*, with at least seven species (Kotlyar, 1984; Deng *et al.*, 1983). Three species, *P. japonicus, P. berndti* and *P. longispina*, occur in Japan and its adjoining waters; *P. kawadae* (Okamura and Ema, 1985) is thought to be a synonym of *P. longispina* (Hayashi, 1993c). Okamura and Ema (1985) reported that *P. japonicus* is distinguished from the other two in Japan by the higher numbers of soft dorsal rays (32–35 vs. 29–32), scales on the lateral line (35–37 vs. 32–34), scales above the lateral line (16–18 vs. 13–15), but these meristic characters do not differentiate *P. berndti* and *P. longispina*.

Larval *Polymixia* is unknown. Recently, Baldwin and Johnson (1995) described and illustrated only head spination of an 11.5 mm SL larva of *Polymixia* sp..

In this study, the first description and illustration of larval *Polymixia* are made on the basis of three specimens of 3.9 mm to 10.0 mm SL. Judging from the small numbers of dorsal-fin rays and scales on an oblique row from the 15th dorsal ray to the lateral line, as described below, the larva of 10.0 mm SL may be *P. berndti* or *P. longispina*.

***Polymixia* sp.**
Figures 16, 17

General Morphology

The body is round in shape and deep in the 3.9 mm postflexion larva, and is moderately deep in the 10.0 mm larva: the body depth at the pectoral-fin base is 46% SL and 36% SL, respectively (Fig. 16). The head is large and round, occupying more than 36% SL. Particularly in the 3.3 mm larva, the head is wide, and the outline of the anterior region of the head from a dorsal view is rectangular. The round eye is large, and its diameter decreases from 50% HL in the 3.3 mm larva to 36% HL in the 10.0 mm larva. The snout is very narrow and slightly protruded. The mouth is inferior, its posterior tip nearly reaching a point beneath the posterior margin of the eye. In the 10.0 mm larva, there are several tiny teeth on



Fig. 16. Larvae of *Polymixia* sp.. A) 3.9 mm SL; B) 10.0 mm SL.

the small premaxilla and about 15 teeth on the dentary. About 20 small, conical teeth appear ventrally on the endopterygoid, which has a half-moon shape. The gut is coiled. The anus is situated posteriorly to mid body, and just before the anal-fin origin, the preanal length occupying 72% SL in the 3.9 mm larva, and 67% SL in the 10.0 mm larva.

The 3.9 mm larva is scaleless. In the 10.0 mm specimen, scales occur on the trunk and tail, but most scales on the lateral surface of the trunk are decidous. Each scale has a spinule projecting backward from the posterior area of the focus at an angle of about 30 degrees to the plate (Appendix Fig. 6). Such larval scales are different from those of trachichthyoids, which have one or more erect spinules on the central area of the scale. Lateral-line scales of larval *Polymixia* of 10.0 mm SL are pored, and each scale has two horizontally parallel, low, smooth ridges on the periphery of the pore. Six scales are present in an oblique row from the 15th dorsal ray to the lateral line, and nine scales from the lateral line to the 9th anal ray. A pair of barbels is present in the hyoid region of the 10.0 mm larva, and each barbel is supported by the first three branchiostegal rays.

Fins and Meristics

In the 3.9 mm larva, the caudal fin has a full complement of principal rays (9 +9). All other fins are forming, but have an incomplete complement of rays. Although five rays of the pelvic fin are countable, an examination of small larvae less than 3.9 mm SL is needed to judge if the fin is precocious, as in some trachichthyoid larvae. The 10.0 mm cleared and stained larva has a full complement of dorsal-fin rays (V, 32), anal-fin rays (IV, 15), pectoral-fin rays (16), and pelvic-fin rays (I, 6). The first rays of the dorsal and anal fins are very short, being present in the body. Additionally, a somewhat wide space intervenes between the first two rays of the fins. No spination appears on fin rays.

The 10.0 mm larva has 28 vertebrae and 7 branchiostegal rays. The first three rays are much shorter than the others and modified (the first and second rays are filamentous and the third is tape-shaped) to support the hyoid barbel.

Pigmentation

The two postflexion larvae have well-developed pigment on the body. In the 3.9 mm larva, punctate and stellate melanophores are scattered on the body, but pigment is sparse on the snout, otic region, base of the pectoral fin, and caudal peduncle. Two small melanophores appear on the lower lobe of the caudal fin. Internal pigment is present on the brain, orbital region and lower limbs of the first two gill arches. In the 10.0 mm larva, the body is dark, and the hyoid barbel is

pigmented, but pigment on the caual fin disappears.

Head Spination

Larval *Polymixia* has moderately-developed head spination, which is similar to that of beryciform larvae, particularly on the parietal, as suggested by Baldwin and Johnson (1995). The 3.9 mm larva examined bears ornamentation on the parietal, pterotic, posttemporal, supracleithrum, opercle, preopercle, and interopercle. In the 10.0 mm cleared and stained larva (Fig. 17), the ornamentation is advanced and complicated, and additional spination occurs on the frontal, extrascapular, suborbitals and subopercle. The frontal has two obliquely oriented, serrate ridges on its posterolateral surface and a smooth ridge anteriorly. The supraorbital ridge moderately protrudes outward, and is serrate on the outer margin. The lachrymal bears no spination, but Baldwin and Johnson's (1995; fig. 4) specimen of 11.5 mm

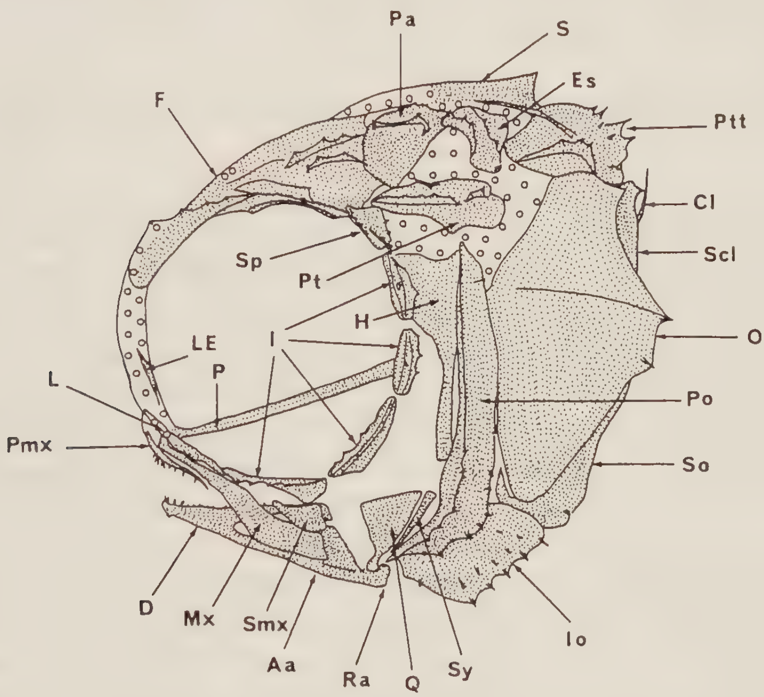


Fig. 17. Head spination of *Polymixia* sp. in 10.0 mm SL. Larger stippling in the figure represents cartilage. F–frontal, LE–lateral ethmoid, L–lachrymal, I–infraorbitals, Sp–sphenotic, Pt–pterotic, S–supraoccipital, Es–extrascapular, Pa–parietal, P–parasphenoid, Pmx–premaxilla, Mx–maxilla, Smx–supramaxilla, D–dentary, Aa–anguloarticular, Ra–retroarticular, Q–quadrate, Sy–symplectic, H–hyomandibular, O–opercle, Po–preopercle, Io–interopercle, So–subopercle, Ptt–posttemporal, Scl–supracleithrum, Cl–cleithrum.

SL has spines on the lower margin of the bone. The first and second infraorbitals bear a serrate ridge on the upper margin, and the third and fourth have tiny spines on the posterior margin. A slightly curved ridge with two spines occurs on the lateral surface of the parietal. The extrascapular has a serrate ridge on the anterior margin and the lateral surface. There are three ridges with serration or spines on the lateral surface of the pterotic. On the sphenotic, there are two serrate ridges and small spines. The arch-shaped preopercle bears a slightly serrate ridge on the anterior margin, and several small spines on the posterior margin at its corner. Three widely-spaced spines occur on the posterior margin of the opercle. An oblique row of needle-like spines is present on the lateral surface and posterior margin of the interopercle. The subopercle has a tiny spine on the posterior margin near the interopercle. The posttemporal possesses a slightly curved, serrate ridge on the lateral surface, and several spines on the posterior margin. A small spine is present on the posterodorsal tip of the supracleithrum. Each of the bones composing the upper and lower jaws has no ornamentation.

INTERRELATIONSHIPS OF THE TRACHICHTHYOIDEI

The systematics of living beryciform fishes were studied by Greenwood *et al.* (1966), Woods and Sonoda (1973), Zehren (1979) and Moore (1993). In their studies, five families, Anomalopidae, Anoplogastridae, Diretmidae, Monocentridae, and Trachichthyidae, are included in the Beryciformes or the related order Trachichthyiformes. Zehren (1979) and Moore (1993) suggested from their osteological studies that the above five families constitute a monophyletic assemblage. From a viewpoint of larval morphology, Baldwin and Johnson (1995) supported Zehren's (1979) and Moore's (1993) hypothesis of monophyly, because "larvae of those families share the presence of tack-like scales and ornamentation on the lateral face of the opercle". Furthermore, Baldwin and Johnson (1995) suggested that presence of supramaxillary spination in larval *Beryx* corroborates Johnson and Patterson's (1993) inclusion of the Berycidae in the Beryciformes rather than Moore's (1993) exclusion of it in his Trachichthyiformes. About the monophyly of the concerned taxa and treatment of the Berycidae, my opinion from larval morphological features described above agrees with Baldwin and Johnson (1995).

In this chapter reproduced from Konishi and Okiyama (1997), relationships of the Trachichthyoidei (Anomalopidae+Monocentridae+Trachichthyidae) are cladistically investigated by the outgroup comparison method on the basis of 26 larval and adult characters described below in detail. Table 1 shows a character matrix for the Trachichthyoidei and their neighboring groups. Based on previously pub-

Table 1. Character matrix for the Beryciformes. 0, primitive; 1, derived state. Parenthesis indicates application of derived character state in the adult stage for body spination. Character numbers are as defined in the text (after Konishi and Okiyama, 1997).

	Character				
	1–5	6–10	11–15	16–20	21–26
Berycidae					
Beryx sp.	00000	00010	00000	0 0 0 1 1	0 0 0 0 0 0
Anoplogastridae					
Anoplogaster cornuta	00000	11000	01111	1 0 0 0 0	0 1 1 1 1 1
Diretmidae					
Diretmoides pauciradiatus	00000	11000	11111	1 1 0 (1) (1)	0 1 1 (1) (1) (1)
Diretmichthys parini	00000	11000	11111	1? 1? 0 (1) (1)	0 (1) (1) (1?) (1?) (1?)
Diretmus argenteus	00000	11000	11111	1 1 0 (1) (1)	0 1 1 (1) (1?) (1?)
Trachichthyoidei					
Anomalopidae					
Anomalops katoptron	00101	00011	00000	1 1 (1) 1 1	(1) 1 1 1 (1) 1
Kryptophanaron alfredi	00101	00011	00000	1 1 (1?) 1 1	1 1 1 1 (1?) 1
Monocentridae					
Monocentris japonicus	00011	01110	00000	1 1 0 1 (1)	(1) (1) (1) (1) (1) (1)
Trachichthyidae					
Aulotrachichthys sp.	11000	00010	00000	1 1 (1) 1 1	1 1 1 1 1 1
Hoplostethus sp.	00000	00000	00000	1 (1) (1) 1 1	1 1 1 1 1 1
Gephyroberyx japonicus	00000	00000	00000	1 1 (1) 1 1	1 1 1 1 1 1
Paratrachichthys sp.	10000	00010	00000	1 (1) (1) (1) (1)	(1) (1) (1) (1) (1) (1)
Optivus sp.	00000	00010	00000	1 1 (1) (1) (1)	(1) (1) (1) (1) (1) (1)

Sources: *Beryx*, present study (PS), Mundy (1990), Baldwin and Johnson (B. & J.) (1995), BSKU 23211; *Anoplogaster*, PS, B. & J. (1995), HUMZ 77473; *Diretmoides*, PS, B. & J. (1995), BSKU 23107; *Diretmichthys*, PS, Kotlyar (1990); *Diretmus*, B. & J. (1995), Zehren (1979); *Anomalops*, PS, BSKU 8879; *Kryptophanaron*, B. & J. (1995); *Monocentris*, PS, B. & J. (1995), BSKU 8844; *Aulotrachichthys*, PS, BSKU 38327; *Hoplostethus*, PS, B. & J. (1995), BSKU 39856; *Gephyroberyx*, PS, BSKU 7237; *Paratrachichthys*, Jordan and Bruce (1993), B. & J. (1995), AMS I.35492-001; *Optivus*, Jordan and Bruce (1993), B. & J. (1995), AMS I.30408-007.

lished hypotheses (Zehren, 1979; Moore, 1993; Baldwin and Johnson, 1995), anoplogastrids+diretmids were selected as the first outgroup for the Trachichthyoidei and *Beryx* as the second.

(*1*) *Position of the anus*—in beryciforms in general, preanal length is relatively more or less shortened during the transition from preflexion to postflexion larvae, but the anus of both preflexion and postflexion larvae is situated just before the origin of the anal fin or posterior to the base of the pelvic fin. In *Aulotrachichthys* (this study; Jordan and Bruce, 1993) and *Paratrachichthys* (Jordan and Bruce, 1993), the anus ontogenetically shifts forward from near the origin of the anal fin to be inserted between the pelvic-fin bases. Large larvae

and juveniles of *Diretmoides pauciradiatus* and *Diretmichthys parini* also exhibit an anterior shift of the anus, but the anus in those taxa is located between the pelvic-fin base and the anal-fin origin (Figs. 5, 7 ; Post and Quero, 1981). The anuses of *Aulotrachichthys* and *Paratrachichthys* are surrounded by black glandular tissue (this study; Jordan and Bruce, 1993), but those of *Diretmoides* and *Diretmichthys* do not have the tissue (this study; Post and Quero, 1981). Homology of the anterior transition of the anus in trachichthyids and diretmids is doubtful. This character is also observed in larvae of the percoid genus, *Acropoma* (Konishi, 1988c), but its occurrence is greatly restricted among teleosts. The ontogenetic shift of the anus anteriorly is a derived character.

(2) *Luminous organs on the ventral margin of the body*—larvae of Japanese *Aulotrachichthys* (Fig. 11) and Australian *Aulotrachichthys* (Jordan and Bruce, 1993) have a luminous organ around the anus and striated tissues ventrolaterally from the pelvic-fin base just beyond the posterior end of the anal-fin base, and on the isthmus inside of the gill cavity. This type of the light organ rarely occurs within teleosts. The presence of the luminous organs on the ventral margin of the body is derived.

(3) *Subocular luminous organ*—larvae of *Anomalops katoptron* have an incipient light organ beneath the eye (Fig. 8). A 6.2 mm NL flexion larva of *Kryptophanaron alfredi* also bears an incipient, rod-shaped light organ on the snout (Baldwin and Johnson, 1995). The presence of subocular light organs is a derived feature within teleosts.

(4) *Luminous organ on the lower jaw*—the 6.5 mm SL larva of *Monocentris japonicus* has a precursor of the heavily pigmented light organ that is present ventral to the tip of the lower jaw (Okiyama, 1988b). The presence of this organ is derived.

(5) *Number of dorsal fins*—*Anomalops katoptron, Kryptophanaron alfredi, Phthanophaneron* (Johnson and Rosenblatt, 1988), *Parmops* (Rosenblatt and Johnson, 1991), *Protoblepharon* (Baldwin *et al.*, 1997) and *Monocentris japonicus* have two dorsal fins. Another anomalopid, *Photoblepharon* (McCosker and Rosenblatt, 1987) and the remaining nine genera of the Beryciformes have a single dorsal fin. The possesion of the two dorsal fins is thus a derived character.

(6) *Absence of dorsal-fin spines*—absence of dorsal-fin spines in the Anoplogastridae and Diretmidae is unique among the Beryciformes. Therefore, this feature is derived, as Zehren (1979) suggested.

(7) *Absence of anal-fin spines*—among beryciforms, only three families, the Anoplogastridae, Diretmidae and Monocentridae, lack spines in the anal fin. As noted by Zehren (1979), the absence of anal-fin spines is derived.

(8) *Three or fewer pelvic-fin rays*—the number of the soft rays in the pelvic fin in the Beryciformes ranges from two to thirteen (usually more than five or six). Three or fewer rays in *Monocentris* is unique.

(9) *Precocious pelvic fin*—early forming pelvic fins occur in larvae of some gadiforms, pleuronectiforms, myctophiforms, beryciforms and perciforms (Ahlstrom and Moser, 1976). In the Beryciformes, *Beryx splendens* (Onishi, 1966), *Anomalops katoptron* (Colin, 1989), *Kryptophanaron alfredi* (Baldwin and Johnson, 1995), *Monocentris japonicus* (Okiyama, 1988b), three Australian trachichthyids, *Aulotrachichthys, Paratrachichthys* and *Optivus* (Jordan and Bruce, 1993), and Japanese *Aulotrachichthys* (this study) have precocious pelvic fins; in *Beryx* and *Anomalops*, the fins appear as buds in the yolk-sac larval stage. The presence of the precocious pelvic fin is derived.

(10) *Pigmentation on the caudal-fin rays*—larvae of *Anomalops katoptron* have pigment on the caudal-fin rays and procurrent spines (Fig. 8). Other anomalopids (e.g., *Kryptophanaron alfredi* of 6.2 mm NL and juvenile *Phthanophaneron harveyi*) also possess this pigment (Baldwin and Johnson, 1995). Other beryciform larvae have an unpigmented caudal fin. The presence of pigmentation on the caudal fin is derived.

(11) *Isolated pigment on the caudal-fin base*—larval diretmids uniquely have a pigment spot on the caudal-fin base, which is isolated from pigment anterior to the caudal peduncle (Figs. 5, 7; Post, 1976; Post and Quero, 1981; Watson, 1996 b). The caudal-fin base of larval *Anomalops katoptron* is also well pigmented, but its pigment is associated with the band of pigment on the head and dorsolateral trunk (Fig. 8). The isolated pigment on the caudal-fin base of larval diretmids is believed to be derived.

(12) *Vertically oriented, prolonged pectoral fin*—the pectoral fin of larvae of the Anoplogastridae (Fig. 3; Okiyama and Hirano, 1988; Watson, 1996a) and Diretmidae (Figs. 5, 7; Post, 1976; Watson, 1996b) is directed upward, its tip approaching the dorsal margin of the trunk. Other teleost larvae (e.g., some myctophiforms, exocoetids, ophidiids, ceratioids, bramids, blenniids, scorpaenids, platycephalids etc.) have prolonged, fan-shaped pectoral fins, but those fins are directed posteriorly. The presence of vertically prolonged pectoral fins in diretmids and anoplogastrids is derived.

(13) *Prolonged parietal spine,* (14) *Prolonged preopercle spine,* (15) *Enlarged supraorbital spine*—presence of those three characters in larvae of anoplogastrids and diretmids is a synapomorphy of those taxa (Baldwin and Johnson, 1995).

(16) *Spinous larval scales*—larvae of *Anoplogaster cornuta, Anomalops katoptron, Monocentris japonicus, Aulotrachichthys* sp., *Hoplostethus* sp., and *Gephyroberyx*

japonicus examined in this study have spinous scales (Figs. 3, 8, 9, 11, 12, 14, respectively). Baldwin and Johnson (1995) noted that presence of spinous scales is a synapomorphy of anoplogastrids, diretmids, anomalopids, monocentrids and trachichthyids.

(*17*) *Ventral scutes*—presence of ventral scutes with spination is rare among adult teleosts. The Beryciformes excluding the Berycidae and Anoplogastridae develop ventral scutes characterized by having spination. Larvae of *Diretmoides, Diretmus, Anomalops, Kryptophanaron, Monocentris, Aulotrachichthys, Gephyroberyx*, and *Optivus* have the scutes, but larval *Hoplostethus* and *Paratrachichthys* do not (Figs. 8, 9, 11, 12, 14; Okiyama, 1988b; Jordan and Bruce, 1993; Baldwin and Johnson, 1995). Shimizu (1990) noted that there is a difference in development of the ventral scutes among adult *Hoplostethus*; scutes are well developed in *H. mediterraneus*, and poorly developed in *H. atlanticus* and *H. melanopus*. Presence of the spiny ventral scutes is derived.

(*18*) *Spination of the maxilla*—maxillary ornamentation in the larval stage is very rare in teleosts, being present in the Lethrinidae (Leis and Rennis, 1983; Johnson, 1984) and some beryciforms. Larval *Aulotrachichthys* develops three spines on the lateral side of the mid-maxilla (Fig. 11). Larval *Beryx* has a downward projecting spine at the anterior portion of the maxilla (Fig. 2; Mundy, 1990), but it is absent in the juvenile stage (Mundy, 1990). Homology of this spination of *Aulotrachichthys* and *Beryx* is doubtful. In larvae of *Anomalops, Kryptophanaron, Hoplostethus, Gephyroberyx, Paratrachichthys* and *Optivus*, maxillary ornamentation is absent (Figs. 8, 12, 14; Baldwin and Johnson, 1995), but adults of *A. katoptron* (BSKU 8879), *Photoblepharon steinitzi* (McCosker and Rosenblatt, 1987), *H. japonicus* (BSKU 39856), *G. japonicus* (BSKU 7237), *Paratrachichthys* (AMS I. 35492-001) and *Optivus* (AMS I.30408-007) bear ornamentation on the maxilla. In the Monocentridae, larvae and adults of *Monocentris japonicus* have no ornamentation on the maxilla (Fig. 10; Baldwin and Johnson, 1995; Zehren, 1979; BSKU 8844), but adult *Cleidopus* possesses the spination (Zehren, 1979). Presence of maxillary spination is derived.

(*19*) *Spination of the subopercle, and* (*20*) *the interopercle*—ornamentation on the subopercle and interopercle is present only in some percoid larvae: serranids, bramids, lethrinids, malacanthids (Johnson, 1984), and some scorpaenids (Moser and Ahlstrom, 1978). Among beryciforms, larvae of *Beryx splendens, Anomalops katoptron, Kryptophanaron alfredi, Aulotrachichthys, Hoplostethus*, and *Gephyroberyx* (Figs. 2, 8, 11, 13, 15; Mundy, 1990; Baldwin and Johnson, 1995) share the derived condition of interopercular and subopercular spination. A 15.7 mm juvenile of *Anoplogaster cornuta* possesses a low ridge without spination on the small, mem-

branous subopercle (Fig. 4), but the adults have no ornamentation on the bone (Zehren, 1979). The subopercular ornamentation of the juvenile *A. cornuta* is different in configuration from that of other beryciform larvae, which have spines and/or spiny ridges. Consequently, homology of this ornamentation of *A. cornuta* and other beryciforms is doubtful. A cleared and stained larva of *Monocentris japonicus* of 8.5 mm SL (Fig. 10) has a single small spine on the subopercle, although it is absent in Baldwin and Johnson's (1995) specimen. Larval *M. japonicus* examined by me and Baldwin and Johnson (1995) have no interopercular spine, but an adult (BSKU 8844) has it. Further, information from adult *Diretmoides pauciradiatus* (BSKU 23107), *Diretmus argenteus* (Zehren, 1979), *Diretmichthys parini* (Kotlyar, 1990), *Paratrachichthys* (AMS I.35492–001) and *Optivus* (AMS I.30408–007) suggests that subopercular and interopercular ornamentation would probably appear in their late larval or juvenile stages.

(*21*) *Spination of the branchiostegal rays*—presence of this spination is uncommon but occurs in larvae of the Priacanthidae (Johnson, 1984) and some beryciforms (this study; Baldwin and Johnson, 1995). Larvae of *Kryptophanaron alfredi, Aulotrachichthys, Hoplostethus* and *Gephyroberyx* share this derived feature (Figs. 11, 12, 14; Baldwin and Johnson, 1995). Larvae of *Anomalops katoptron* (Fig. 8), *Monocentris japonicus* (Fig. 9), *Paratrachichthys* and *Optivus* (Baldwin and Johnson, 1995) lack ornamentation on the branchiostegal rays, but adults of those taxa have it. It probably appears in the late larval or juvenile stage. This feature is absent in larval and adult *Beryx splendens* (Fig. 1; Baldwin and Johnson, 1995; BSKU 23211), but adult *Centroberyx* in the Berycidae has it (Zehren, 1979; BSKU 2344).

(*22*) *Spinules on the dorsal-fin rays,* (*23*) *anal-fin rays,* (*24*) *caudal-fin rays,* (*25*) *pectoral-fin rays, and* (*26*) *pelvic-fin rays*—presence of spinules on the fin rays of larvae is very rare, occurring in some priacanthids (Konishi, unpubl.), *Zanclus cornutus* (Johnson and Washington, 1987) and some beryciforms (this study; Baldwin and Johnson, 1995). Distribution of fin spination of larvae and juveniles in each taxon of beryciforms is as follows: in anoplogastrids, all fins (this study); in two diretmid genera, *Diretmoides* and *Diretmus*, the dorsal and anal fins (Baldwin and Johnson, 1995); in two anomalopid genera, *Anomalops* and *Kryptophanaron*, the dorsal, anal, caudal and pelvic fins (this study; Baldwin and Johnson, 1995); in three trachichthyids, *Aulotrachichthys* sp., *Hoplostethus* sp. and *Gephyroberyx japonicus*, all fins (this study; Baldwin and Johnson, 1995). An examination of adults of *Diretmoides pauciradiatus* (BSKU 23107), *Anomalops katoptron* (BSKU 8879), *Monocentris japonicus* (BSKU 8844), *Paratrachichthys* (AMS I.35492–001) and *Optivus* (AMS I.30408–007), and published information for

Diretmus argenteus and *Photoblepharon palpebratus* (Zehren, 1979), reveal evidence that these genera develop the spination on all fins. Therefore, I believe that the ontogenetic acquisition of spinules on rays of all fins is derived. It is present in all beryciforms examined except *Beryx*.

By cladistical analysis with the PAUP 3.1 program, two equally parsimonious trees of the relationships of the Beryciformes were obtained. Figure 18 is a consensus tree. From figure 18, it is evident that the 13 genera examined here constitute a monophyletic assemblage diagnosed by two derived characters; presence of spination on the subopercle and interopercle (characters 19, 20). These characters are reversed in *Anoplogaster cornuta*.

Anoplogaster cornuta in the Anoplogastridae, *Diretmus argenteus*, *Diretmoides pauciradiatus* and *Diretmichthys parini* in the Diretmidae, *Anomalops katoptron* and *Kryptophanaron alfredi* in the Anomalopidae, *Monocentris japonicus* in the Monocentridae, *Aulotrachichthys* sp., *Paratrachichthys* sp., *Optivus* sp., *Hoplostethus* sp. and *Gephyroberyx japonicus* in the Trachichthyidae form a monophyletic group, as mentioned by Zehren (1979), Moore (1993), and Baldwin and Johnson (1995). Their larvae (or juveniles) have seven synapomorphies: spinous scales (character 16), ventral scutes (character 17), spinules on the dorsal fin (character 22), anal fin (character 23), caudal fin (character 24), pectoral fin (character 25) and pelvic fin (character 26). Character 17 is reversed in *Anoplogaster*.

The Anoplogastridae and Diretmidae share six derived features: absence of dorsal- and anal-fin spines; possession of a dorsally directed, prolonged pectoral fin; a nearly vertically extended parietal spine; a posteroventrally directed, prolonged preopercular spine; and an enlarged supraorbital spine (characters 6, 7, 12, 13, 14, 15, respectively).

Two synapomorphies, presence of spination on the maxilla (character 18) and the branchiostegal rays (character 21), indicate that the Trachichthyoidei (Anomalopidae+Monocentridae+Trachichthyidae) are monophyletic, however Zehren (1979) reported that there are no adult derived characters unique to those three families. In addition, Zehren (1979) suggested that the Monocentridae are more closely related to the Trachichthyidae than to the Anomalopidae, but none of the 26 derived characters cited in support of that relationships is unique (Zehren, 1979). Moore (1993) also considered monocentrids and trachichthyids to be sister groups on the basis of a single unique synapomorphy of the subocular shelf restricted to the third infraorbital. Since the condition of the subocular shelf is modified in anomalopids due to the presence of the light organ, this character may not be appropriate to discuss the relationships within trachichthyoids. In my phylogeny (Fig. 18), the Anomalopidae appears to be the sister group of the

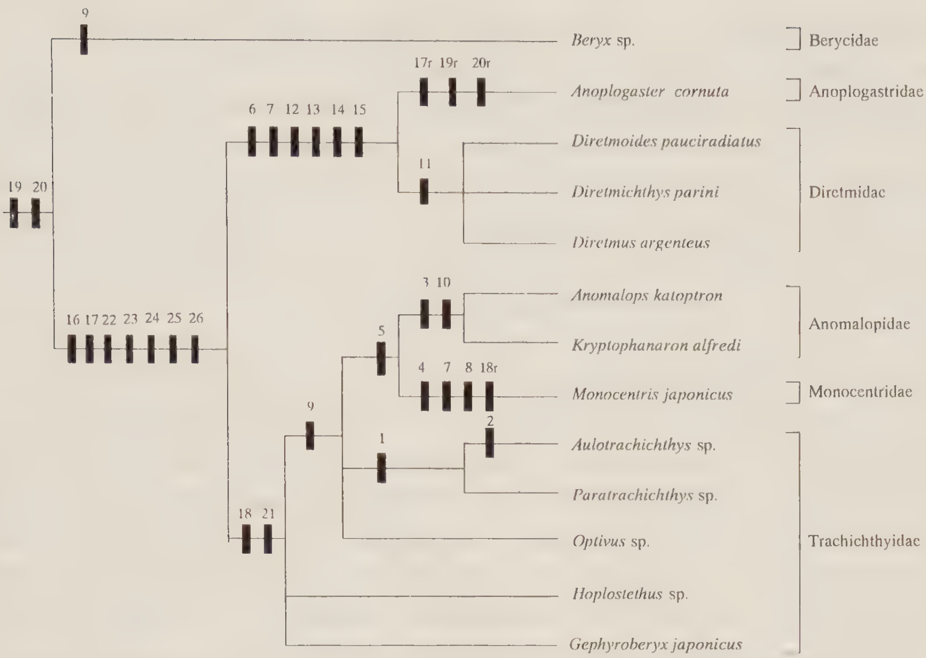


Fig. 18. Cladogram showing hypothesized relationships among trachichthyoids and their neighboring groups (after Konishi and Okiyama, 1997). Numbers refer to characters described in the text. "r" shows reversal.

Monocentridae; those families share a single derived feature, presence of two dorsal fins (character 5). One anomalopid genus, *Photoblepharon*, has a single dorsal fin with only two spines (II, 18–19) versus two dorsal fins with several spines (IV- to VI-I, 14 to 16) in *Anomalops*, *Kryptophanaron*, *Phthanophaneron* (Johnson and Rosenblatt, 1988), *Parmops* (Rosenblatt and Johnson, 1991) and *Protoblepharon* (Baldwin *et al.*, 1997). A single dorsal fin with a reduced number of spines is unique among trachichthyoids to *Photoblepharon*, and it is autapomorphic for that genus (Johnson and Rosenblatt, 1988).

Baldwin and Johnson (1995) reported that larval *Kryptophanaron* and *Monocentris* share the presence of large scales and pigment on and between the three to four anteriormost dorsal-fin spines, and noted that those features are not present in other beryciform larvae examined. In my specimen of a 5.8 mm SL larva of *Anomalops katoptron* (Fig. 8), it seems that the scales are not so large in comparison with those of three trachichthyid larvae (Figs. 11, 12, 14). But, since the longitudinal scales (about 27) of the larva of *A. katoptron* are considerably fewer than the adult complement of about 60 (Abe, 1951), they are large relative to adult scales. Further, pigment on the anterior portion of dorsal fin is lacking (Fig. 8). Baldwin and Johnson (1995) did not observe that pigment in other beryciform

larvae, but my specimen of larval *Diretmichthys parini* (Fig. 7) has pigment on the proximal region of first three elements (soft rays) of the dorsal fin.

Figure 18 shows that the Trachichthyidae (*Aulotrachichthys*+*Paratrachichthys*+*Optivus*+*Hoplostethus*+*Gephyroberyx*) may be paraphyletic, a possibility also suggested by Baldwin and Johnson (1995). No autapomorphy of the Trachichthyidae was found in this study, but Moore (1993) cited two adult autapomorphies: a posteriorly pointing spine on the posttemporal, and a modal number of six procurrent spines in the upper caudal-fin lobe and either five or six spines in the lower caudal-fin lobe. That spine on the posttemporal also appears in *Centroberyx* (Moore, 1993; BSKU 2344). Fujita (1990) reported that three Japanese trachichthyids possess 6 to 8 procurrent spines in the upper caudal-fin lobe and 6 or 7 in the lower one, and *Anoplogaster* has the same number of procurrent spines (7 in the dorsal side, 6 or 7 in the ventral side). Therefore, Moore's (1993) two characters are not unique to the Trachichthyidae. In this study, three trachichthyids, *Aulotrachichthys, Paratrachichthys* and *Optivus*, share with anomalopids and monocentrids the precocious pelvic fins (character 9), a feature lacking in larval *Hoplostethus* and *Gephyroberyx*. Further study of the Trachichthyidae is needed.

In general, ornamentation in the form of spinous elements develops on most exposed head bones, scales, fins and branchiostegal rays in the larval stage of the Beryciformes. Adult beryciforms retain most of the larval spination, and sometimes develop additional ornamentation on some bones (e.g., the opercular series, infraorbitals and both jaws). Similar ornamentation present in some percoid larvae is reduced after the larval or juvenile stages, and is usually absent in adults. In beryciforms, it is difficult to categorize ornamentation as "larval spination" or "adult spination" except for the huge spines of the parietal and preopercle in larval anoplogastrids and diretmids, and the spinous scales in the larval stage, and thus I considered all life history stages when coding head and body spines as "present" or "absent." Comparative study of the development of ornamentation among larval beryciforms reveals that there is variation in timing in the development of spination, i.e., heterochrony, and further investigation of the patterns of development in trachichthyoids may shed more light on relationships within the group. Other potentially informative characters from larvae also need further study. For example, preflexion larvae of *Anoplogaster cornuta, Diretmichthys parini, Gephyroberyx* sp., *Paratrachichthys* sp., *Optivus* sp. (Figs. 3, 7, 14; Jordan and Bruce, 1993), *Hoplostethus* sp. and *Zeus faber* deposited in the Australian Museum possess an extremely interesting feature: the dorsal- and anal-fin bases are present in the finfold, being isolated from the body. This character appears in the larvae of lower taxa such as the Argentinoidei (Ahlstrom *et al.*, 1984), Stomiatoidea (Kawa-

guchi and Moser, 1984) and Myctophidae (Moser *et al.*, 1984). This feature may be present in anomalopid and monocentrid preflexion larvae, as suggested by the hypothesized monophyly of these two families, anoplogastrids, diretmids and trachichthyids.

In conclusion, I emphasize the need for supplementary data from larvae, juveniles and adults to elucidate the phylogeny of the trachichthyoids.

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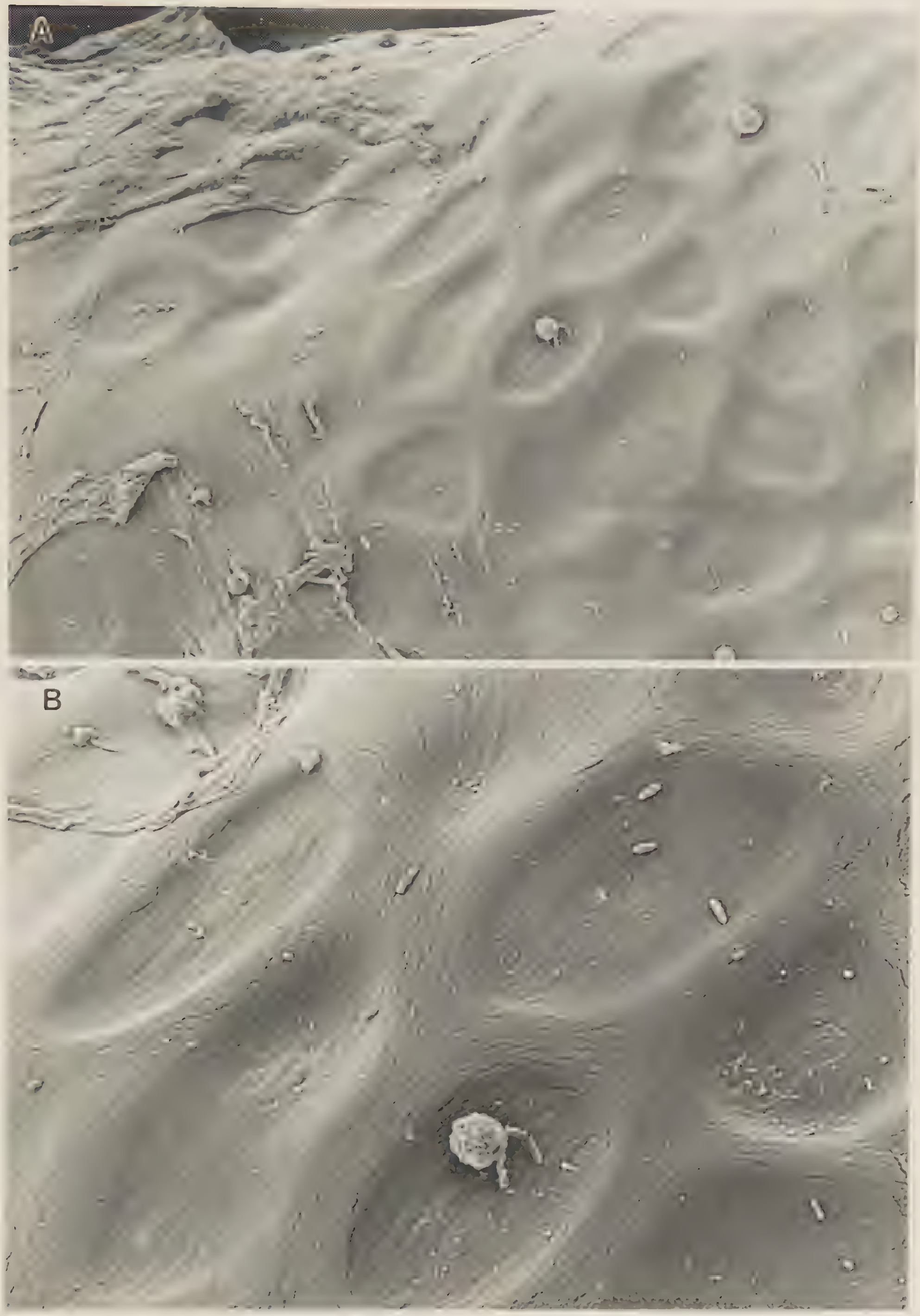
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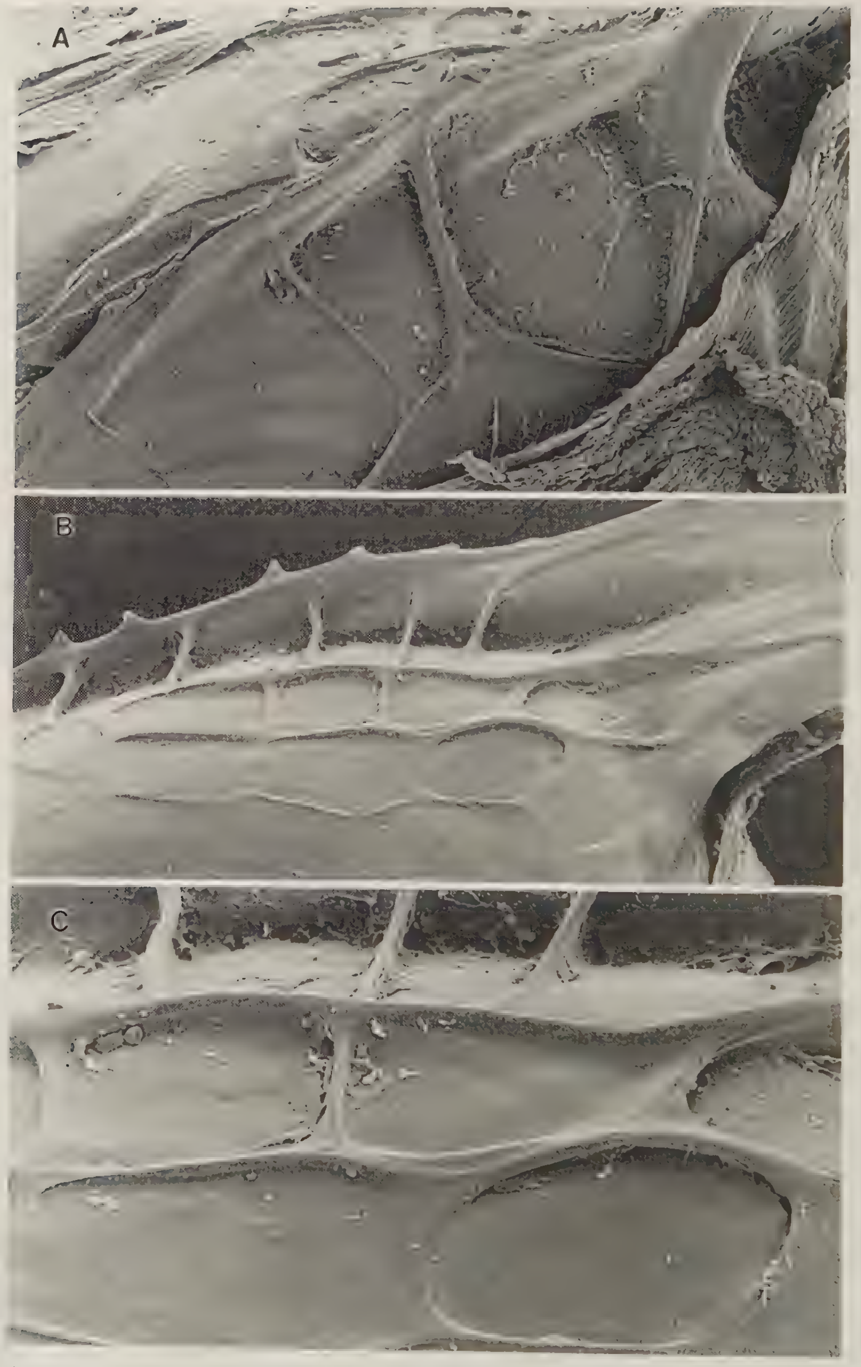
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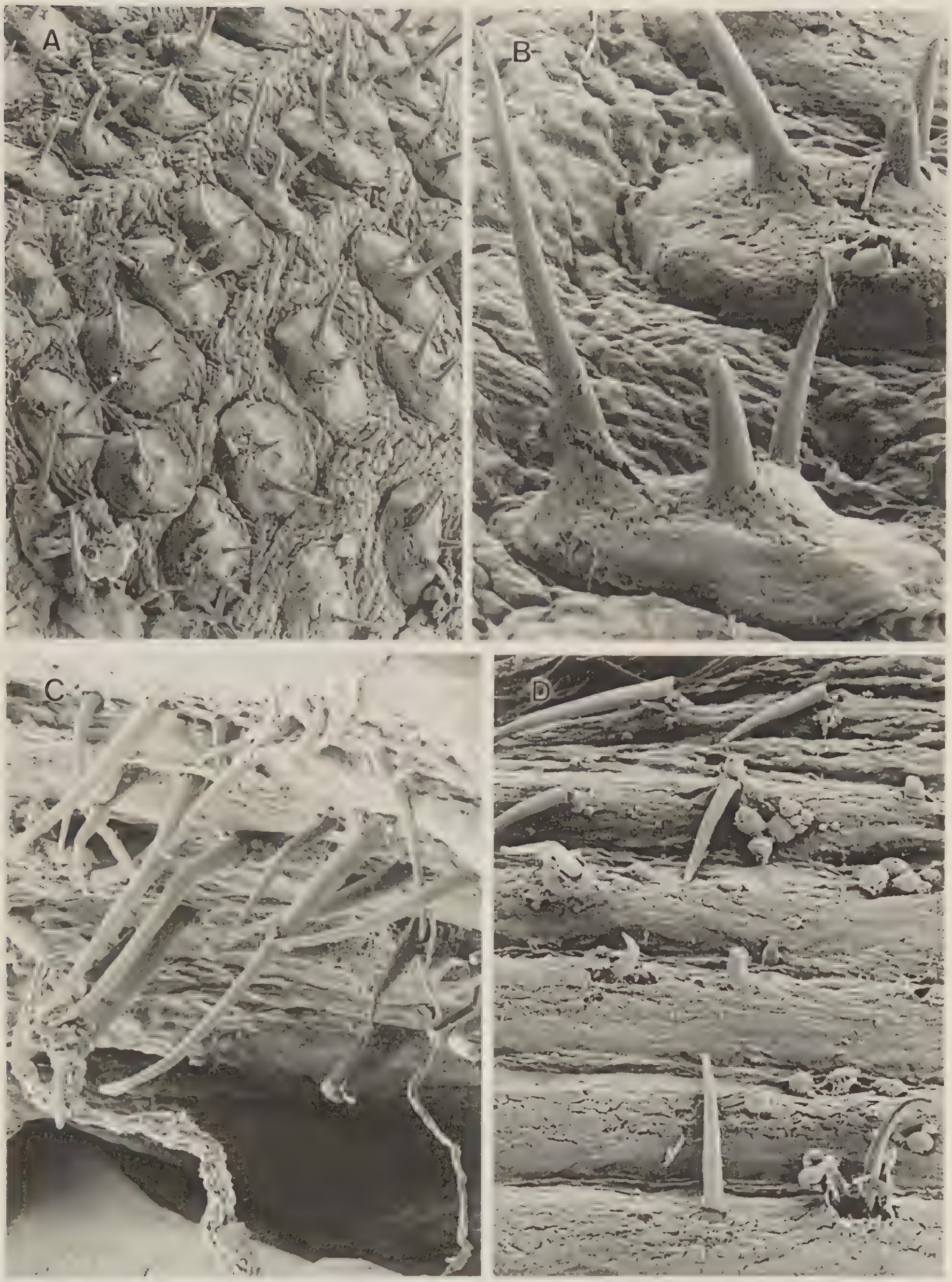
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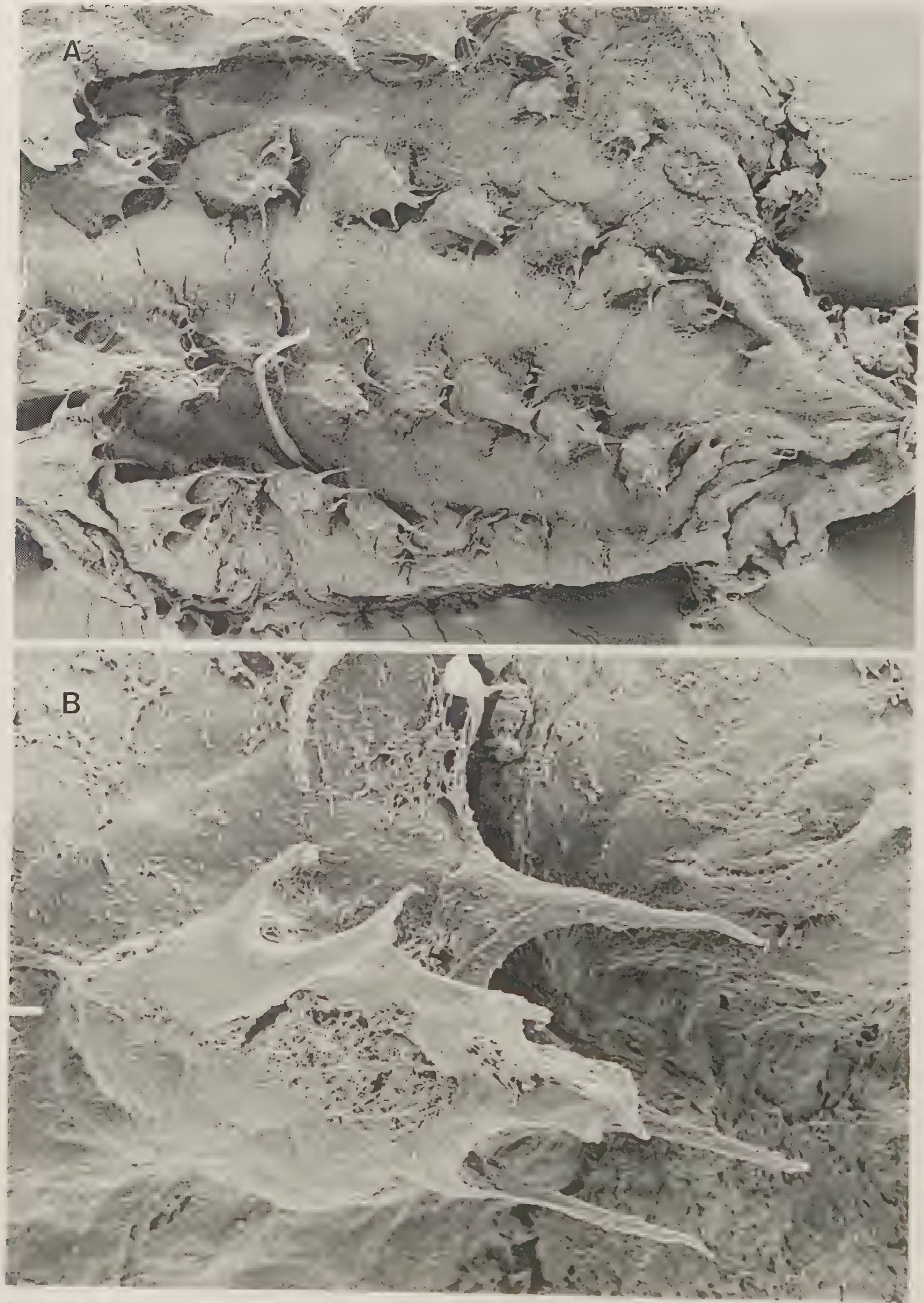
Appendix Figure 1. Scanning electromicrographs (SEM's) of the dorsolateral surface of the frontal of a larval *Beryx* sp. in 8.0 mm SL. A) ×400 ; B) ×1,000.



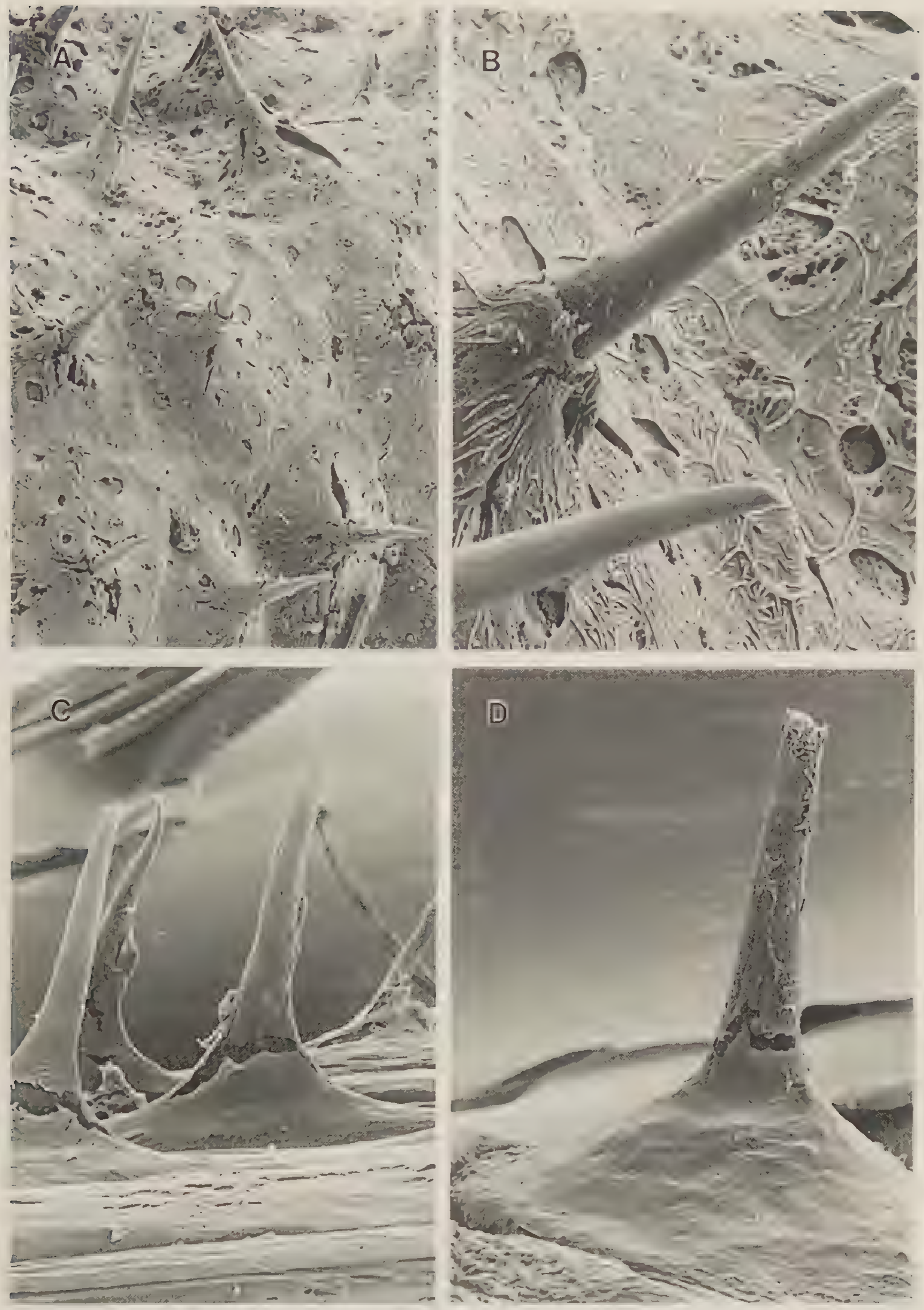
Appendix Figure 2. SEM's of the base of the parietal spine of anoplogastrid and diretmid larvae. A) *Anoplogaster cornuta*, 5.7 mm SL, ×100; B) *Diretmichthys parini*, 6.4 mm SL, ×100; C) *D. parini*, 6.4 mm SL, ×250.



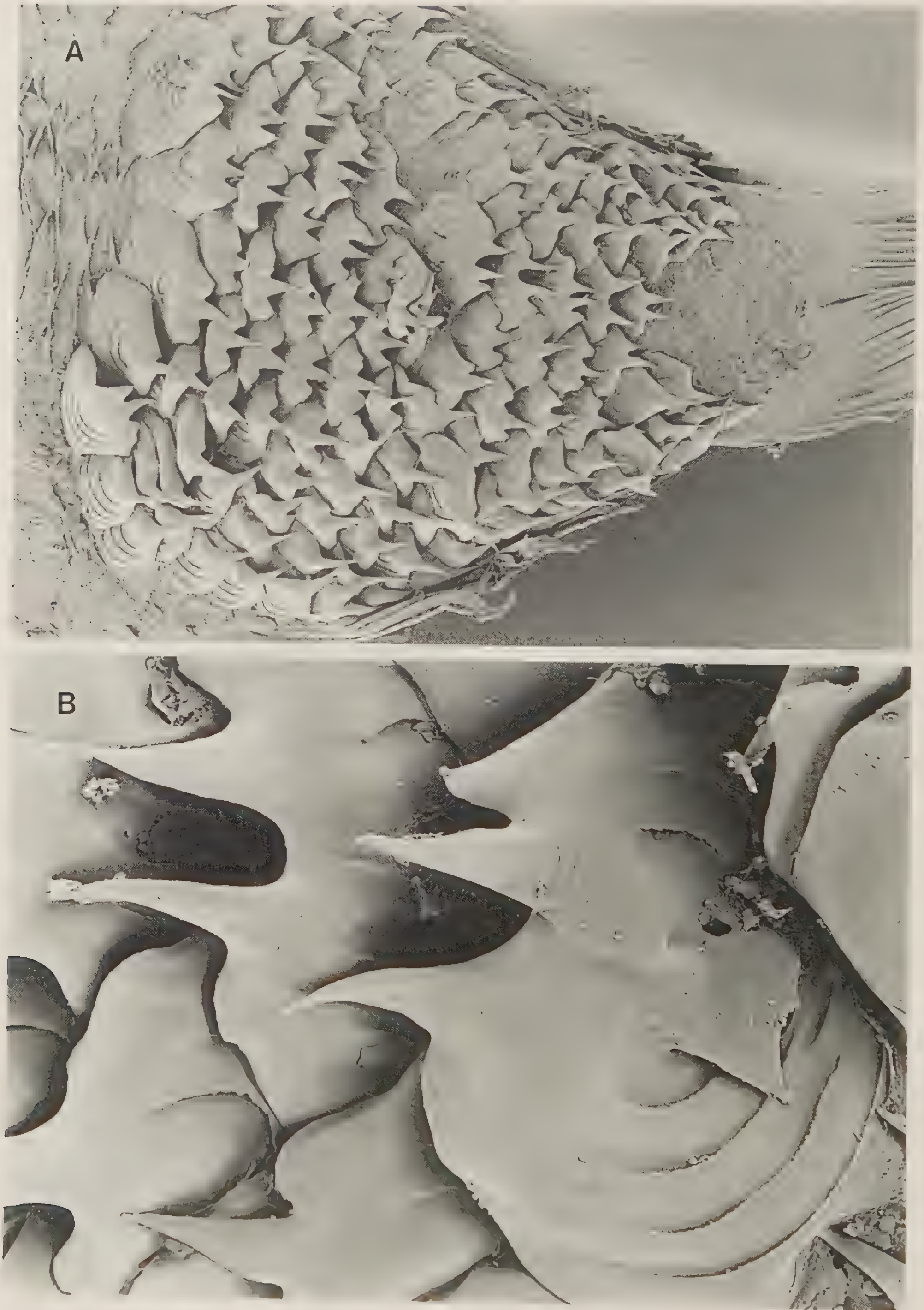
Appendix Figure 3. SEM's of spinous scales and spinules on fin rays of a larval *Anomalops katoptron* in 5.8 mm SL. A) scales, ×100; B) scales, ×400; C) spinules on pelvic-fin rays, ×400; D) spinules on caudal-fin rays, ×400.



Appendix Figure 4. SEM's of spinous scales of a larval *Monocentris japonicus* in 5.7 mm SL. A) ×50; B) ×400.



Appendix Figure 5. SEM's of spinous scales and spinules on dorsal-fin rays of a larval *Hoplostethus* sp. in 10.7 mm SL. A) scales, ×150; B) spinules on scales, ×700; C) spinules on dorsal-fin rays, ×350; D) a spinule on the dorsal-fin ray, ×400.



Appendix Figure 6. SEM's of scales of a larval *Polymixia* sp. in 6.0 mm SL. A) ×35; B) ×200.

キンメダイ目魚類幼期の形態発育史とヒウチダイ亜目の類縁関係

小西　芳信

抄　　録

キンメダイ目 Beryciformes の魚類幼期の形態的知見は，一部の種類を除いてきわめて貧弱であり，本目の類縁関係を論じるほど蓄積されていない．本研究では，キンメダイ目を構成するキンメダイ科 Berycidae，オニキンメ科 Anoplogastridae，ナカムラギンメ科 Diretmidae，ヒカリキンメダイ科 Anomalopidae，マツカサウオ科 Monocentridae，ヒウチダイ科 Trachichthyidae，イットウダイ科 Holocentridae の7科のうち，イットウダイ科を除く6科をとりあげ，種分化が顕著な西部太平洋から得た9属9種の幼期の形態を記載した．また，幼期の形態的特徴と成魚のそれから選んだ26の派生的形質に基づいて，ヒカリキンメダイ科，マツカサウオ科，ヒウチダイ科の3科からなるヒウチダイ亜目 Trachichthyoidei とその周辺グループの類縁関係を検討した．なお，幼期の形態記載には，幼期の知見が乏しくキンメダイ目への帰属に問題を残しているギンメダイ科 Polymixiidae の1種も含めた．

研究に供した幼期の標本は計39個体で，これらの形態は実体顕微鏡下で観察した．一部の標本は，軟・硬骨二重染色法及び走査型電子顕微鏡により体表の棘要素を詳細に観察した．また，成魚の形態観察も補足的に行った．

幼期の形態記載

キンメダイ科キンメダイ属の1種 *Beryx* sp. では，臀鰭基部長は長く，背鰭及び早生性の腹鰭の第1軟条は顕著に伸長する．黒色素胞は，孵化直後の仔魚では体全体に発達するが，後期仔魚期では貧弱である．頭部諸骨に棘要素が見られ，特に額骨，涙骨，鰓蓋骨のそれらは形状において特異的である．オニキンメ科オニキンメ *Anoplogaster cornuta* では，体はやや肥厚する．鰭条はすべて軟条からなり，背鰭及び臀鰭の原基は鰭膜中に出現する．腹鰭は非早生性で，脊索上屈後仔魚の胸鰭は垂直近くに伸長する．背鰭，臀鰭，尾鰭，腹鰭の鰭条に小棘が出現する．鱗は腹鰭前方の体腹面に偏在して見られ，個々の鱗は棘性鱗で垂直に立つ1小棘を有する．黒色素胞は，軀幹部及び尾部の外縁を除く体のほぼ全域を覆う．頭部の棘要素のうち，ろ頂骨，前鰓蓋骨，眼上骨の伸長棘が特徴的である．ナカムラギンメ科チゴナカムラギンメ *Diretmoides pauciradiatus* では，鰭条のすべては軟条からなり，腹鰭は非早生性で，胸鰭は後上方に伸長する．鰭条の小棘は背鰭と臀鰭に見られる．棘性鱗と稜鱗が腹部前方の腹正中線上とその周辺に出現する．黒色素胞の発達は緩慢で，尾柄部後方の黒色素斑は本科幼期に特異的に出現する．ろ頂骨，前鰓蓋骨，眼上骨上の伸長棘が特徴的である．ナカムラギンメ *Diretmichthys parini* の形態の発達過程とその特徴は，チゴナカムラギンメのそれとほぼ同様であるが，黒色素胞はより発達する．また，背鰭及び臀鰭の原基が膜鰭中に出現する特徴を有する．ヒカリキンメダイ科ヒカリキンメダイ *Anomalops katoptron* では，早生性の腹鰭は伸長し，背鰭，臀鰭，尾鰭とともに，これらの鰭条に小棘が見られる．鰓条骨にも小棘が出現する．鱗は棘性鱗で，頭部を除く体全体を覆う．腹部の腹正中線上に稜鱗が並ぶ．眼下に1つの大きな発光器がある．黒色素胞は頭部から尾部の体の背方で帯状に見られるほか，吻端，下顎下面，腹鰭にも出現し，尾鰭条のそれは，キンメダイ目幼期のなかでは特異的である．頭部諸骨は小棘か鋸歯状の低い隆起脉で覆われ，伸長棘や大きな棘は見られない．マツカサウオ科マツカサウオ *Monocentris japinicus* では，臀鰭条はすべて軟条で，早生性の腹鰭の条数（I，3）は本目のなかでは特異的である．下顎先端下面に黒色を呈した発光器がある．ピラミッド形をした特異な形態の鱗が体を覆い，軀幹部腹正中線上に稜鱗が見られる．黒色素胞は腹鰭，背鰭前方部を含め体全体に出現する．頭部の棘要素のなかでは，額骨，ろ頂骨上の側方に張り出す柄状

突起が特徴的である．ヒウチダイ科ハリダシエビス属の1種 *Aulotrachichthys* sp. では，腹鰭は早生性で，他の鰭も含め鰭条に小棘がある．鰓条骨にも小棘が見られる．鱗は直立する1―2本の小棘を持ち，腹部腹正中線上に稜鱗がある．胸鰭基部下方及び喉部から臀鰭後端の体腹縁に縞状発光器がある．肛門は腹鰭基部の間に位置する．黒色素胞は体全体を覆い，特に腹鰭は黒い．頭部の棘要素はすべての露出骨でよく発達し，特に後側頭骨と前鰓蓋骨隅角部の棘は特徴的である．ヒウチダイ属の1種 *Hoplostethus* sp. では，腹鰭は非早生性で，他の鰭と同様に鰭条に小棘をともなう．鰓条骨にも小棘が見られる．鱗は1―2本の直立棘を持つ．黒色素胞は体全体に散在すると思われる．頭部の棘要素の発達程度は，ヒウチダイ科の他の2種に比べやや緩慢である． ハシキンメ *Gephyroberyx japonicus* では，背鰭・臀鰭の原基は膜鰭中に出現する．腹鰭は非早生性で，他の鰭も含む鰭条と鰓条骨に小棘が見られる．鱗は棘性鱗で，腹部腹正中線上に稜鱗が並ぶ．黒色素胞は体全体を覆う．頭部の棘要素は発達し，特にろ頂骨と前鰓蓋骨隅角部の各1棘はやや伸長する．ギンメダイ科ギンメダイ属の1種 *Polymixia* sp. では，体は丸くやや肥厚する．腹鰭は比較的小さな個体で見られる．鱗には直立する小棘がない．頤に1組の髭が出現する．体は全体が黒色素胞で濃密に覆われる．頭部の棘要素はやや発達し，特に背方のそれは形状においてキンメダイと似る．

ヒウチダイ亜目の類縁関係

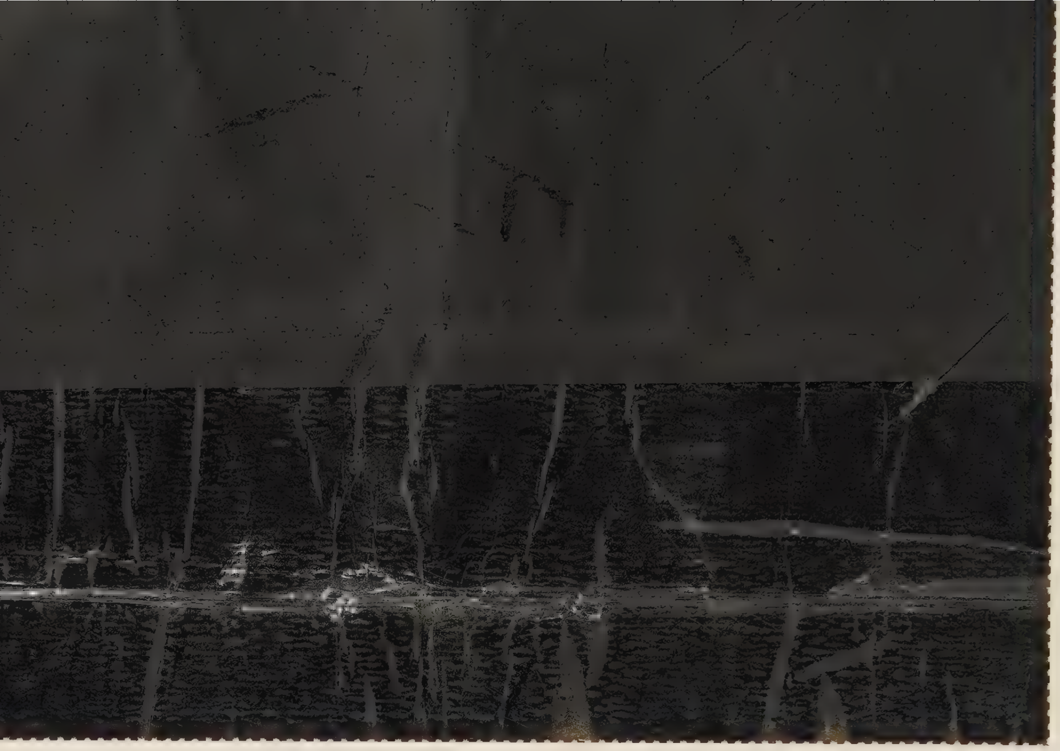
26の派生的形質（肛門位置，発光器の有無，背鰭の数，背・臀鰭条の無棘化，腹鰭条の少数化，腹鰭の早生性，尾鰭の鰭条と基部上の黒色素胞の存在，体各部における棘要素の有無）に基づいて，分岐分類的解析を行った結果，1） オニキンメ科， ナカムラギンメ科，ヒカリキンメダイ科，マツカサウオ科，ヒウチダイ科の5科は単系統群である，2）オニキンメ科とナカムラギンメ科は姉妹群である，3）ヒカリキンメダイ科，マツカサウオ科，ヒウチダイ科の3科は単系統である、とする従来の説を支持する．そして，新たに，4） ヒカリキンメダイ科とマツカサウオ科は姉妹群である，5）ヒウチダイ科は偽系統的であることが示唆された．4）と5）の結果は，マツカサウオ科とヒウチダイ科との姉妹関係及びヒウチダイ科の単系統性を説く成魚の形態比較の結果と異なる．

非　売　品

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